ANIMAL HEALTH, PRODUCTION AND PASTURE

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Foreword

Sir John Hammond, C.B.E., M.A., D.Sc., F.R.S.

In most countries in the world, including New Zealand, Australia, Africa and South America, the production of milk, meat and wool depends largely and sometimes entirely on the amount and quality of grassland and its products; this dependence is exemplified by the advanced methods of grassland management practised in New Zealand. During the last fifteen years the dairy, beef and sheep industries in Great Britain, Europe and the North American continent have turned to grass and grass products to supply much more of the protein requirements for cattle and sheep, largely as a sequel to the absence or severe shortage of imported feeding-stuffs during the last war. This has involved new methods of increasing the output of our grassland, new systems of management and increased stocking rates.

Each step in intensification has raised new problems to be solved before full and safe use could be made of them, and not the least of these was the effect of the changes on the health of the animal. This book will supply a long-felt want in not only giving an account of the new methods used in the intensification of grassland production but also of the hazards involved by these methods on the health of the animal and most important, methods of control for the various nutritive and parasitic diseases concerned.

Editors' Preface

The suggestion that a book should be written with the object of bringing together, between one set of covers, the sum of our knowledge of the factors which influence the health and productivity of the grazing animal was first made by Sir James Scott Watson. To him we owe a special debt of gratitude. At a stage when we are passing from what may be called the 'pasture establishment era' into the 'pasture use era' it seemed appropriate to Sir James that a volume should be published which would both summarize existing knowledge on pasture use and, by doing so, indicate the gaps that remain. Such a volume, it was thought, would prove to be a useful reference for farmers, students and veterinarians, and a stimulus to agricultural and veterinary research workers and advisory officers.

Thanks to the patient co-operation of all the contributors the volume is now ready. Knowledge concerning the health and productivity of grazing animals is, of course, far from complete, and therefore we need make no apology for the fact that this book provides answers to some of the problems only. We can claim, however, that reflected in its pages is the accumulated knowledge of a group of workers, experienced in their various fields in several countries, whose efforts have been directed to achieving increased health and productivity in grazing flocks and herds. We are extremely grateful to all of them for the time and effort that they have given to this project.

Ministry of Agriculture, Fisheries and Food Bulletin No 48 and *Agriculture Journal*, for their permission to reproduce figures or tables

By the happy coincidence of his return to the United Kingdom, we were able as the book reached the proof stage, to obtain the help of Mr Donald W Jolly, M R C V S, whose knowledge of editorial matters has contributed enormously to the rapid and smooth transformation of manuscript to text The task of editing this book has not been an easy one, and but for Mr Jolly's support and the encouragement and co-operation of Longmans, Green and Co, it would have been immeasurably more difficult

We gratefully acknowledge the advice and assistance of Ruth Allcroft, O B E, Ph.D, B Sc, whose excellent review 'The Use and Misuse of Mineral Supplements' (*Vet Rec* 73, 1255, 1961) provided the basis of the section on selenium We are also grateful to the Editor of the *Veterinary Record* for allowing us to make liberal use of the review

We are also indebted to Mr K. N Burns, B Sc, M R C V S, of the Central Veterinary Laboratory, Ministry of Agriculture, Fisheries and Food, Weybridge, Surrey, for the section on the industrial contamination of pasture

CHAPTER ONE

Introduction

A. N. WORDEN, K. C. SELLERS AND D. E. TRIBE

General Introduction—Disorders of the foot in grazing animals; foot-rot, strawberry foot-rot, red foot, foot-abscess, foul of the foot—Recent findings of potential importance, facial eczema, silica, selenium—Industrial contamination of pasture; fluorosis, other contaminants—Ecology of the grazing animal—General observations.

It is approptiate that a book concerned with agricultural production should start by reminding the reader of the critical situation which now faces mankind—a situation which has been aptly summarized in the phrase 'population explosion'. It is against the stark background of over-population and food shortage that man's endeavours must now be viewed, and if society is to find a solution to this overwhelmingly important problem there is no doubt that the farmer, and the body of scientists that now support him, must together play a key role. Also there are still vast areas of the world, even in the so-called well-developed countries, where the application of new techniques can increase greatly the output of food. In view of the fact that the world's most important crop by far is 'grass' (by which we mean the plant communities used by grazing animals), and the world's most important food-producing animals are ruminants, which depend largely, and frequently exclusively, on grass for their lifetime nutrition, any techniques for improving the production or utilization of grass are likely to bring about the most rewarding increases in the supply of food for the human population. The exciting and tremendous potential of the world's grasslands was well illustrated in the group of plenary papers which were read at the Eighth International Grassland Congress in 1960.

McMeekan (1952, 1956, 1960) and many others have pointed out that in the past too little attention was paid to the problem of pasture use but now it is becoming generally accepted that 'The productivity of grassland in terms of meat, milk, wool or hides as sale crops, must be viewed as an integral part of a pastoral enterprise, in which the nutritional demands of the ruminant animals are met for 365 days in the year and for the whole duration of its productive life' (Davies, 1960) It remains theoretically true that the most important single advance in the economy of pasture use would be the replacement of the grazing animal altogether by chemical methods of processing grass into food for humans However, 'the grilled grass steak is a very long way from achievement' (Melville, 1960) and there is no doubt that, during the foreseeable future, grass will have to be processed through the ruminant animal before the human population can derive much benefit from it

Although grass is the world's most important crop, it is paradoxically of almost no direct use to man as a source of food In fact, the only sections of the animal kingdom that can derive much nutritional benefit from grass are those which have undergone a marked evolutionary change in the structure and function of some part of their alimentary tract, and which, in consequence, can accommodate a large intestinal population of bacteria and protozoa. It is this large and varied microbial population that converts the many refractory constituents of grass, which would otherwise remain indigested, into readily available sources of energy, protein, or vitamins Herbivores such as the horse and the rabbit accommodate their microbial populations towards the dorsal end of their alimentary tracts, but the ruminant, which appears to exhibit the most advanced evolutionary adaptation to cope efficiently with a bulky, coarse grass diet, accommodates its populations in the large diverticulum of the foregut, the reticulo-rumen The complex symbiotic relations between the micro-organisms and the host ruminant have been well summarized by Annison and Lewis (1959)

In view of the ruminant's dependence upon the processes of microbial breakdown and synthesis it is permissible, although of course it is an over-simplification, to regard grass primarily as a substrate for micro-organisms rather than as a food for cattle and sheep Many of the nutritional deficiencies of grass then become immediately obvious The substrate in any successful industrial bacterial fermentation process needs to be constant in quantity and quality These requirements are

far from being met by the diet of the grazing animal. The quality of pasture is constantly changing, and, in most pastoral areas of the world, it changes over a very wide range. The intake of herbage similarly alters and is affected by a large and varied number of independent and interacting factors. Moreover in an industrial fermentation process the environment within the fermentation chamber must be maintained at a constant equilibrium, not only by controlling the quantity and quality of the substrate, but also by controlling the rate of removal of the bacterial metabolites, by maintaining constant and uniform mixing of the fermenting mass, by diluting the mass to a constant dry-matter content, and by controlling the range of micro-organisms that are active in the fermentation process and eliminating undesirable types. The analogy with the rumen is clear, and serves to illustrate the importance in this situation of the processes of absorption and rate of passage of food from the reticulo-rumen, of rumen motility and rumination, of salivation and of the factors which regulate the type and size of microbial population in the rumen and determine its variation. The precise control of these factors by the farmer or grazier is clearly impossible, but it is towards this ideal that those who manage the grazing animals must work. However, 'a fuller knowledge leads to a fuller control' and the range of research, and the diversity of specialized interests required to make our knowledge of pasture utilization more complete is exceptionally wide.

The biochemist, physiologist and microbiologist have an important part to play in revealing what may be called the 'normal' situation; in the investigation of rumen dysfunction, and, in a wider sense, the dysfunction of the grazing ruminant, veterinary knowledge must also be used. Since the research findings of all of these workers has, at some stage, to be interpreted in terms of the management of the grazing animal, the agricultural scientist has his own contribution to make. The purpose of the present volume is to bring together specialists from the various disciplines working in this broad field, in order to review the results of the enormous amount of research that has been carried out particularly in the last fifteen years, and to summarize the extent of our present knowledge in the subject.

It is recognized that our knowledge of the problems of producing grass and of managing pastures outstrips our knowledge of the problems of animal production from grass and of managing the grazing animal. Nevertheless enormous progress has been made since, during

the last war Sir Joseph Barcroft and his colleagues at Cambridge initiated their fundamental investigations into the physiology of the rumen and about the same time Dr C P McMeekan and his New Zealand colleagues intensified and extended their studies on grazing management and since veterinary research workers in many parts of the world turned with renewed vigour to the problems of the metabolic parasitic and nutritional diseases of grazing stock It is the purpose of this book to review the advances that have been made at the same time realising that this will be the first word on the subject and not the last It is because no other volume has attempted to cover this important but wide and complex field that this book was required In a rapidly developing field such as this it is inevitable that there are gaps in the story and that in some instances different authors have expressed conflicting views Indeed it has been our object not only to present what is known on the subject but also to indicate where there are deficiencies and uncertainties in our knowledge It is hoped therefore that this book will stimulate further work so that future volumes will be more comprehensive We are grateful to the eminent workers who have responded to our appeal and who have collectively submitted a series of chapters that cover a great deal of existing knowledge and an extremely wide range of experience

In the selection of particular fields of work for inclusion in this book we have been guided by several considerations Firstly it was decided to include material only if directly relevant to the grazing animal For this reason the fields of infertility and genetics although both important in a general sense as factors influencing the efficiency of production of the grazing animal are not included Similarly although a wide range of infectious diseases e g mastitis tuberculosis pleuropneumonia and foot and mouth disease may greatly impair the productivity of grazing animals the fact that they are grazing or are consuming grass does not materially affect the course of the disease and therefore these conditions have not been considered in the present context There is however one particular group of infectious conditions for which an exception can be made the group which cause disorders of the feet In this case the microclimate produced by the vegetation in which the animal stands together with the type of grazing management that is practised may exert such a profound influence upon the incidence and severity of the disorders that brief mention of them is required

DISORDERS OF THE FOOT IN GRAZING ANIMALS

CONTAGIOUS FOOT-ROT OF SHEEP AND GOATS

There are several diseases of the foot of sheep; Beveridge (1959) believes that the term 'foot-rot' should be reserved for the specific condition which he defines as a contagious disease of the sheep's foot characterized by separation of a large portion of the hoof from the soft tissues due to a spreading infection immediately beneath the horn, and caused primarily by *Fusiformis nodosus*. The goat is recognized as the only other susceptible animal.

Foot-rot has long been established as the most prevalent cause of lameness in most of the sheep-carrying areas of the world. Beveridge (1941), in establishing that *F. nodosus* was the primary causal agent, showed that this organism does not occur naturally apart from the feet of affected animals. He regarded *Spirochaeta penortha* as an accessory causal agent and a third type of organism, a mobile fusiform, is constantly present in lesions of foot-rot but is not of established significance in the causation of the disease nor confined to affected feet. The infective agent of foot-rot does not survive for long anywhere except in the feet of sheep or goats showing some lesions, and Beveridge was able to demonstrate successful eradication procedures based upon this finding.

In view of his important contribution to the understanding of, and to the method of controlling, this disease, Beveridge's views on foot-rot may be quoted almost verbatim. Foot-rot behaves as a typical specific infectious disease in that it does not arise spontaneously. This point is of vital importance because many sheepmen and veterinarians think that the disease will make its appearance whenever conditions are favourable; in other words, that it is a non-specific infection resulting from sheep running in damp, lush pasture. This notion has arisen because in the flocks in the endemic areas the infection is constantly present and the spread and prevalence of the disease is influenced by the seasonal and pastural conditions, for foot-rot can spread from sheep to sheep only in certain environmental circumstances.

Predisposing factors necessary for the spread of foot-rot are prolonged wetness of the feet or injury to the skin between the digits by any agent such as grass seeds or larvae of the nematode, Strongyloides spp. Damp, lush pasture is favourable to the spread of the disease whereas free water, as in marshes, is not. Warm water is more favourable than cold. Thus outbreaks of the disease occur most commonly in spring

and autumn on rich pasture In these circumstances the sheep may develop a condition popularly known as 'scald' This is a non-specific superficial inflammation of the skin between the digits The cause of 'scald' has not been established In itself it is not serious and usually clears up spontaneously, although it may cause lameness for a few days Scald provides an ideal portal of entry for the causal agents of foot-rot, and when some animals in the flock are carrying the infection an outbreak of foot-rot follows the 'scald'

Sheep of all ages are infected, lambs become infected rather more readily than older animals but the disease is less severe The Merino is more susceptible than the British breeds, although the latter are not particularly resistant

The method of control devised by Beveridge (1941) has stood the test of time, not only in Australia itself, but also in New Zealand (Ensor, 1957), Italy (Coppino, 1951), and England (see Beveridge, 1959)

The principle to be followed is to segregate all affected animals and any suspected of carrying the infection and then place the remaining healthy sheep on a pasture that has not had infected sheep on it for at least two weeks The infection can live in mud and on pasture for some days but not as long as two weeks If many of the flock are affected a concerted effort should be made to cure them by repeated treatment before carrying out the final eradication procedure This eradication procedure should be done when the incidence of the disease is low and when climatic and pastural conditions are not conducive to the spread of the disease, that is to say, in the driest time of the year

In order to eradicate the disease it is necessary to impress on the farmer that the object is to eliminate all trace of infection and not merely to deal with lame sheep All sheep in the flock must be caught and their feet examined closely and if necessary trimmed It is essential to segregate not only those showing lesions of foot-rot but also any showing moist, inflamed hairless skin between the digits Such animals may carry the infection for months without the hoof being affected Misshapen hoofs should be trimmed and searched for small pockets of infection. Those sheep found healthy should be passed through a foot-bath of 5 per cent formalin before being placed on the fresh pasture The sheep with foot-rot and the suspected carriers should be either sold for slaughter or kept in isolation while undergoing treatment. When cured they should be held for a further month and re-examined before being returned to the healthy flock because relapses often occur in sheep that appear to have been cured It has been suggested that

relapses may be less likely to occur after treatment with chloramphenicol than after formalin.

The detailed procedure to be followed in eradicating the disease from a particular farm needs to be adapted to local conditions. Reasonably good facilities are essential for success and it is unsatisfactory to work in a muddy yard. A shearing shed is the ideal place to do the work. Re-introduction of infection is, of course, always through sheep or goats, so that any new-comers should be examined carefully and, if necessary, treated and isolated before being allowed to join, or to graze upon the same land as the main flock. Littlejohn (1961) has adopted the methods of Beveridge to British farming conditions and has reported a successful eradication from 15 commercial flocks.

STRAWBERRY FOOT-ROT IN SHEEP

This condition has been reported from Scotland by Harriss (1948) and appears to be a mycosis: Thomson (1954) was able to isolate an organism now known as *Dermatophilus pedis* (Ainsworth and Austwick, 1959). Affected animals develop what may become an extensive inflammatory swelling of the foot from the coronet upwards, followed by thick crust formation. A variety of treatments has been employed but none so far has been reported as influencing favourably the natural course of the disease.

RED FOOT OF LAMBS

Red foot is a widely distributed condition of new-born lambs in southern and central Scotland and is therefore a disease manifested in the progeny of grazing animals. It has been described by Greig (1951), who believes that it is neither infectious nor hereditary in origin. It appears to have a varied incidence from flock to flock, and may disappear from a given flock for a number of years despite any known changes in management practices. The incidence in affected hirsels is said rarely to exceed 15 per cent. Red foot may be seen just after birth and is confined to young lambs. The horn of the hoof becomes detached, with the exposure of red, sensitive tissue. There are sometimes ulcerated areas in the mucous membrane of the mouth. No means of effective treatment is known, and destruction is advised, since the lamb although otherwise healthy in appearance is so crippled that it cannot follow the ewe.

FOOT ABSCESS (DIGITAL SUPPURATION) IN SHEEP

Foot abscess is the name given to a suppurative condition associated with *Fus formis necrophorus* infection (Gregory 1939) Beveridge (1959) differentiated it from foot rot and Belschner (1950) emphasized that it was mainly confined to adult sheep in contrast to foot rot to which all ages of sheep are susceptible

FOUL OF THE FOOT IN CATTLE

This is a form of necrobacillosis associated with *Fus formis necrophor s* infection Although sometimes referred to as foot rot it is aetiologically distinct from the condition in sheep and goats described to which cattle are insusceptible (Beveridge 1941) The condition occurs sporadically throughout the world mainly in dairy cattle and has a marked local variation in incidence Certain farms may suffer more severely than others and the disease may be particularly prevalent in certain years (Beveridge 1959 Grant Millar and Worden 1942)

Flint and Jensen (1951) made a detailed study of the pathology of 116 cases supplemented by attempted reproduction of the syndrome and concluded that the condition was a necrotizing infection of the tissues immediately proximal to the coronary band or of the interdigital tissues often complicated by arthritis of the coffin joint and caused in part by *F ecrophorus* penetrating from the surface This fits in with the conception that environmental factors other than the existence of the infection are important particularly trauma Beveridge (1959) states that stony and muddy paths are considered to be conducive to the disease which may also follow the jamming of a foreign body between the d gits Until the availability of sulphonamides local treatment was the rule This was difficult and had often to be prolonged Marked success from sulphonamide therapy has been reported from 1946 onwards and today this is widely employed (usually by intravenous injection of sulphadimidine alone or in conjunction with other sulphonamides) despite the report by Roberts Kiesel and Lewis (1948) to the effect that the great majority of cases are self limiting and that the response to intravenous glucose in their series were not significantly different from that to sulphonamides

RECENT FINDINGS OF POTENTIAL IMPORTANCE

A further important consideration which guided us in the selection of subjects for inclusion in this volume was the present state of our

knowledge in relation to a particular subject. It will be obvious to the reader that we have not limited our choice of subjects to those in which our knowledge is now complete, but only those subjects have been included which are sufficiently advanced, and about which sufficient research has been published, to enable a critical and balanced review to be written. It is for this reason that scant attention has been paid to that group of conditions which have a wide distribution throughout the world and which are referred to by descriptive names such as 'ill-thrift', 'unthriftiness' and others. Although the economic importance of such conditions is indisputable it is not yet possible to characterize them on a rational basis. Frequently such conditions are confused by a complex situation which may involve over-stocking, parasitism, saline water, minor element deficiencies and an inadequate caloric intake. Our policy has meant that a number of recent findings, potentially of great importance, but, at the moment of uncertain significance, have had to be excluded. The following section serves to draw the reader's attention to such findings and to indicate the direction of possible developments in the future.

FACIAL ECZEMA

This is an important disease of grazing sheep and cattle which has occurred widely in the North Island of New Zealand since the end of the last century and, during the last two or three years serious outbreaks have been reported from the Gippsland district of Victoria, Australia. To those acquainted with the disastrous consequences of this disease in which whole flocks may be decimated and farmers forced to leave their properties, it may appear incongruous to put this disease in the present category. However, although the importance of the disease can scarcely be overrated in the localities in which it occurs, it is a condition which, in terms of the world's grasslands, is of a restricted importance. Indeed its significance in the long-term may turn out to be that it is an outstanding example of a disease of grazing animals known to be caused by a disease of pasture plants.

During the last fifty years an immense amount of research into the disease has been performed by veterinary workers in New Zealand, and the various steps in the unravelling of the problem have been traced by Filmer and Johns (1960). Eventually the combined efforts of a large team, which included plant as well as veterinary pathologists, chemists, biochemists, agronomists, veterinary clinicians, and physiologists, resulted in the discovery that the disease was associated with the

ingestion by grazing stock of a liver-damaging factor, now called sporidesmin produced by a saprophytic fungus, *Pithomyces chartarum* (Berk and Curt) M B Ellis, which commonly infects certain graminaceous pasture plants during warm humid weather Measures for controlling facial eczema are still being investigated but it is hoped that it will be possible to develop a suitable vaccine to protect the animals, and suitable fungicides or techniques of pasture management to protect the plants.

In many parts of the world results of facial eczema research have stimulated workers to consider the possibility that other plant or soil fungi may produce substances which are toxic to grazing animals There exists the possibility, for example, that diseases characterized by acute photosensitization and jaundice, such as 'geeldikkop' in South Africa and 'alveld' in Norway, might be caused by fungal toxins

SILICA

It has been pointed out by Baker, Jones and Milne (1961) that silicon and its compounds are ubiquitous constituents of the diet of the grazing animal Sheep ingest large quantities of both soluble and insoluble silica, the amounts depending largely upon the plant species in the available herbage and on their stages of development A good deal of the soluble silica is absorbed as silicic acid and is normally excreted in the urine Insoluble silica occurs in plants as opal phytoliths (Smithson, 1958) and apparently most of it passes undigested through the alimentary tract to be excreted in the faeces However, it has been suggested (Baker, Jones and Milne, 1961) that a fraction of the opal phytoliths together with an assortment of other allothigenic particles, pass through the epithelium of the alimentary tract of grazing ruminants, and arrive, possibly via the lymphatics, in the bladder, where they act as nuclei for the deposition of authigenic opal during the formation of uroliths Future work is clearly needed in order to test and substantiate this interesting speculation, but there is little doubt that by applying mineragraphic techniques to a problem of animal health these workers have opened up a new and promising field of enquiry

It has been suggested that ingested opal phytoliths may be of importance to the grazing ruminant in at least two other directions Baker, Jones and Wardrop (1961) have suggested that the presence in the rumen of abrasive opal phytoliths, and other particulate matter, may play an important part in the erosion of certain areas of the rumen

epithelium. Also, some evidence has been published (Baker, Jones and Wardrop, 1959) in support of the theory that attrition by opal phytoliths in pasture plants and soil may be a major cause of wear in sheep's teeth. Because excessive wear of incisor teeth of sheep grazing improved pastures in New Zealand and Australia is a problem of considerable economic importance (see e.g. Barnicoat, 1959) this concept is of more than academic interest.

SELENIUM

Before the identification (Schwarz and Foltz, 1957; Patterson, Milstrey and Stokstad, 1957) of selenium as an integral constituent of 'Factor 3' (a previously unknown agent protecting rats against dietary necrotic liver degeneration) the only veterinary interest in this element was related to the disorders and losses in stock resulting from consumption of herbage containing toxic amounts of selenium. The most well-known distribution of seleniferous soils and vegetation is in the western half of the U.S.A., but wheat containing 1 to 2 p.p.m. selenium has been obtained from many other parts of the world (Trelease, 1945), and small seleniferous areas have been found in Eire (Walsh, Fleming, O'Connor and Sweeney, 1951) and in Australia (Knott, McCray and Hall, 1958).

The naturally occurring disorders are known as 'alkali disease' and 'blind staggers' and were thought to be manifestations of chronic and acute selenium poisoning respectively (Moxon and Rhian, 1943), but more recent work suggests that both these syndromes come within the category of chronic selenosis. Rosenfeld and Beath (1946) reported that blind staggers in cattle in Wyoming is caused by selenium poisoning. This syndrome is considered to be identical with polioencephalomalacia, a non-infectious disease of cattle and sheep on pasture and feedlot in Colorado and is known as 'forage poisoning', the cause of which has not been determined (Jensen, Grimer and Adams, 1956). The absence of the clinical signs described as characteristic of chronic selenium poisoning (Moxton and Rhian, 1943) in the cattle population in Colorado where polioencephalomalacia is common, is irreconcilable with the theory that this disease is caused by selenium poisoning (Jensen *et al.*, 1956). Maag, Orsborn and Clopton (1960) reported that seleniferous plants can produce either acute or chronic poisoning, the toxic effect depending on the type of selenium compound present, the type of experimental animal, the criterion of toxicity and the experimental conditions. To determine the effect of sodium selenite

on cattle under typical feedlot conditions, Maag *et al*, fed a ration of ground grain, alfalfa hay and molasses plus selenium (as sodium selenite) from 0 25 to 0 50 mg per pound bodyweight over a period of 28 weeks Few signs typical of alkali disease, blind staggers or forage poisoning developed, cumulative effects were not produced at the lower level of the Se dosage In earlier studies the ill-effects of feeding seleniferous plants to livestock have been attributed solely to the presence of selenium in the plants Maag *et al* (1960) suggest that alkaloids and other toxic substances which have been found in many of the seleniferous plants may cause the syndromes attributed to selenium poisoning in cattle and sheep

The report of Maag *et al* (1960) and the well-known fact that the toxicity of selenium is influenced by dietary factors such as the protein content of the diet and other constituents (Moxon and Rhian, 1943) suggests that the toxicity of selenium for cattle and sheep should be re-investigated under conditions pertaining to its use under different conditions and in particular areas This is particularly important now that selenium has been shown to be involved in essential biological functions of many of our domestic animals and in view of the similarity of the lesions in polioencephalomalacia and those in cerebrocortical necrosis in cattle and sheep (Terlecki and Markson, 1961)

Schwarz and Foltz (1958) showed there is a marked difference in the biopotency of selenium compounds They divided them into three main categories with respect to biopotency against liver necrosis in rats, (a) elementary selenium and certain inorganic and organic compounds are practically inactive, (b) a second group including most inorganic selenium compounds such as selenate and selenite, many organic selenium compounds, and also the selenium analogues of cystine, cystathionine and methionine which have a 50 per cent effective dose (ED_{50}) of about 0 02 to 0 03 p p m Se (2 to 3 μg per cent Se), (c) the third group of higher biopotency is small and so far only four synthetic organic compounds have been found to be more active than selenite but none of them reaches the biopotency of 'Factor 3' which has an ED_{50} of about 0 7 μg per cent Se A daily dose of 0 1 μg of Factor 3-Se fully protects rats against death and significantly enhances growth. This requirement is in accordance with amounts of selenium found in natural foods which are of the order of 0 05 to 10 μg per g of dry matter An estimation of selenium does not give an estimation of 'Factor 3' activity since some foods contain the element in a biologically inert form, Factor 3-selenium is

the most effective selenium compound thus far known (Schwarz and Foltz, 1958).

In a recent review Schwarz (1960) clarified some of the relationships of selenium and vitamin E. So far, there appear to be three groups of diseases which must be separated:

(1) Those caused by vitamin E deficiency which are not influenced by Factor 3-selenium even in large excess; resorption sterility in rats and encephalomalacia in chicks come into this category. (2) Those caused by Factor 3-selenium deficiency which are not affected by vitamin E, such as a disease entity in rats comprising lack of growth, muscular wasting, adrenal atrophy and pancreatic dystrophy, and also a growth effect in the chick. (It appears that a growth effect in the lamb can be added to this list—see following discussion.) (3) Those caused by a simultaneous deficiency of both factors. To this group belong dietary liver necrosis in the rat, liver necrosis and muscular dystrophy in the pig, multiple necrosis in the mouse, heart and peripheral muscular dystrophy in the mink, and exudative diathesis in chicks and turkeys.

Thus, dietary liver necrosis is essentially the result of the simultaneous lack of Factor 3-selenium and vitamin E and although a lack of either of these factors alone often produces relatively mild chronic diseases, the simultaneous deficiency of both leads invariably to acute tissue damage and to death. Methionine and cystine, when supplied at levels exceeding the requirement for growth, may delay the onset of liver necrosis as a result of a sparing effect on the requirement for vitamin E but they do not prevent it (Schwarz, 1960). The clarification of these relationships may help to explain some of the complexities and anomalies reported in liver necrosis and muscle degeneration syndromes in pigs. Schwarz points out that a number of diseases hitherto attributed solely to vitamin E are of a dual origin and that the presence or absence of Factor 3-active selenium determines the fate of an animal on a vitamin E deficient diet.

In the last few years it has been demonstrated that Se plays an important role in the prevention of muscular dystrophy and poor thriving conditions in sheep and calves. Muth, Oldfield, Schubert and Remmert (1959) showed that the incidence of white muscle disease in lambs was significantly reduced when their mothers were fed on a ration previously known to produce the condition and to which 0·1 p.p.m. Se (as sodium selenite) was added; addition of vitamin E to the diet was without effect. In a later experiment, Oldfield, Muth and Schubert (1960) reported that addition of 0·1 p.p.m. Se to a ration for

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ewes from the third month of pregnancy onwards or intramuscular injection of 1 4 mg Se to lambs soon after birth (in both instances as sodium selenite) prevented white muscle disease and resulted in increased growth of lambs as compared with untreated controls The growth response of the lambs was greater when Se was fed pre-natally than when it was injected post natally Large doses of vitamin E at birth protected lambs from white muscle disease but did not result in improved growth

Results of trials in New Zealand (McLean Thomson and Claxton, 1959, Drake, Grant and Hartley 1960) confirmed and supplemented the Oregon reports α tocopherol was of no value when given to pregnant ewes 1 to 3 weeks before lambing whereas 5 mg Se (as sodium selenate) given once orally reduced the number of peri natal deaths of lambs caused by white muscle disease administration of 1 mg Se orally to lambs 2 to 3 weeks after birth almost completely prevented the disease and 300 mg α tocopherol gave some protection In a large number of field trials it was found that oral administration of three 5 mg doses of Se (as sodium selenate) to lambs 5 to 8 months of age accelerated weight gains and reduced mortalities on farms where unthriftiness in weaned and unweaned lambs was high This unthriftiness (hogget ill thrift) is an entity which commonly occurs in early autumn in weaned lambs grazing lush pasture and is an important cause of economic loss in the New Zealand sheep industry Later reports (N Z Dept Agric Rep 1959–60) indicate that administration of 5 mg Se at monthly intervals to ewes from one month before tupping to just before lambing greatly increased the lambing percentage decreased the number of barren ewes and eliminated congenital white muscle disease on farms where there is often a concomitant barren ewe problem as well as congenital white muscle disease

Oral doses of small amounts of selenium prevented muscular dystrophy in calves in areas of North Scotland (Sharman Blaxter and Wilson 1959) where earlier work (Blaxter and Sharman 1953 Sharman 1954) had demonstrated that relatively large doses of α-tocopherol were necessary to prevent the disease A later report (Blaxter, McCallum Wilson Sharman and Donald 1961) confirmed that administration of selenium by oral or subcutaneous routes was effective in reducing the incidence of muscular dystrophy in calves and that the α tocopherol given orally was slightly but not significantly less effective, a single injection of 15 mg Se as sodium selenite within a few days of birth or injection of 5 mg selenium at 3-week intervals from birth afforded

considerable but not complete protection in two groups of 51 calves; 5 mg. selenium by mouth at 3-week intervals from birth afforded complete protection to a third group of 51 calves.

This brief review indicates some of the diverse effects of selenium—harmful when too much is present in the diet and beneficial when very small supplements are added to rations which cause certain disease entities. As yet it is too early to say whether these latter rations are deficient in selenium since the determination of trace amounts of selenium is difficult and satisfactory analytical methods have only recently been worked out. It appears too that there may be variations in the optimal requirements of selenium relative to its various physiological effects, and these will have to be determined for different classes of stock.

It is obvious also that selenium is a toxic element since small amounts in the food may cause chronic poisoning. However, Schwarz (1960) has pointed out that the minimum chronic toxic dose of selenite selenium is approximately 300 to 400 µg. per 100 gm. of diet (3 to 4 p.p.m.) and if this level is compared with that which protects against Factor 3-deficiency, then selenium is relatively not more toxic than many other dietary constituents. The ratio between effective dose and toxic dose is of the order of 1 to 100 which compares favourably with the therapeutic indices of amino-acids, salts and almost all other important nutrients (Schwarz, 1960). But no one would deny that considerable caution should be used concerning the therapeutic or prophylactic use of selenium and that the safest method of supplementation would be by parenteral administration. In New Zealand, the use of the element has, by regulation, been brought under professional control and in the United States of America its use is regulated under the Food Additives (Delaney) Amendment of the Pure Food and Drugs Act. It would therefore seem sensible that steps should always be taken to prohibit the use of selenium in mineral mixtures, as an additive in compound foodstuffs, or as fertilizer for top-dressing purposes. These precautions, however, should not hinder investigations into its possible beneficial effect in livestock.

INDUSTRIAL FLUOROSIS

The occurrence of fluorosis in cattle and sheep grazing in the vicinity of industrial undertakings has been reported during the last 50 years in many European countries, Great Britain and the United States of America. In 1912 Bartolucci described an outbreak in cattle

associated with a superphosphate works in Italy and Roholm's classical treatise on fluorosis in man and animals was published in 1937 The first detailed investigations in Britain were carried out during 1937–39 on farms in the brickfield area of Bedfordshire (Blakemore, Bosworth and Green, 1948), followed a few years later by another investigation into fluorosis associated with aluminium works at Fort William in Scotland (Boddie, 1949) During the post-war expansion of industry the incidence of fluorosis increased in several areas in Britain, two of the most important being the steel-making area in south Yorkshire (Towers, 1954) and the Potteries of north Staffordshire

Industries which have been associated with fluorosis in Britain include (1) Steel-making when large amounts of fluorspar are used, mainly in basic open hearth furnaces, (2) brick-making in several areas, but particularly in the vicinity of the large concentrations of kilns in the south-eastern Midlands of England, (3) ceramic works, colour and vitreous enamelling processes using fluoride as fluxes, (4) open-air calcining of ironstone which may contain calcium fluoride, (5) aluminium production by electrolytic reduction of alumina

Coal-burning plants are a potential source but are rarely sufficiently concentrated to produce a damaging level of fluorosis, though dental lesions in cattle can often be found in the neighbourhood of large coal-burning establishments (Burns and Allcroft, unpublished data)

The toxicity of fluorine compounds is related to their solubility, their concentration in the diet and the length of time over which they are ingested Thus fluorine in the form of sodium fluoride is the most toxic and in the form of calcium fluoride least toxic In feeding-stuffs for cattle the lower limit of toxicity of soluble fluorine is usually regarded as being in the range of 30–50 p p m fluorine in the dry matter of the total diet, the comparable level for the less soluble compounds such as rock phosphate would be almost twice as much as this (N R C, 1960)

The level of fluorine contamination of herbage varies widely and pasture analyses alone are not sufficient to assess the degree of fluorosis in the animal Factors affecting the level of deposition include (a) the amount and duration of the fluorine emissions and their proximity to pasture (b) the influence of local topography and weather, particularly the prevailing wind, and (c) the type of vegetation and its rate of growth Herbage samples from uncontaminated areas usually have fluorine values of less than 10 p p m DM but levels found in fluorosis areas frequently range from 30 to 300 p p m and in some

instances the very high values of 2,000 p.p.m. on grass and 3,000 p.p.m. on kale have been recorded.

An evaluation of an animal's fluorine status should be made from the analysis of animal material used to confirm the clinical assessment. Urinary fluorine levels are a reflection mainly of current intake and output. Normal urine contains less than 10 p.p.m. fluorine (at SG. 1.030). In fluorosis areas values are usually over 10 p.p.m., commonly 20–50, sometimes higher, and values over 100 have occurred. In most fluorosis areas, however, there may be periods of relatively light contamination when urinary fluorine may be in the normal range.

The concentration of fluorine in the bone reflects the amount of fluorine ingested over the period involved and therefore bone fluorine levels are the most useful guide to the animal's fluorine status. Normal bone levels are less than 1,000 p.p.m. on ash, levels between 2,000 and 4,000 usually indicate some exposure and levels in excess of 4,000 are frequently associated with lameness. In fluorosis areas bone fluorine content is commonly 6,000–10,000 p.p.m. and sometimes as much as 20,000 (Allcroft, 1959).

The classical and characteristic changes of fluorosis are the dental lesions and these include yellow, brown or black staining, hypoplasia of enamel and teeth and excessive and irregular wear of incisors and molars. Dental enamel is only affected by ingested fluorine during the developmental stage so that teeth already fully formed at the time of the fluorine intake remain normal. The distribution of dental lesions throughout the various age-groups in a herd may thus be used to estimate the onset and duration of the intake.

In cattle the severity of dental lesions usually found is not sufficient to interfere with feeding or with drinking cold water, but may prejudice the sale of an animal, whereas in sheep dental deformity particularly of cheek teeth, may be very detrimental to health and condition (Boddie, 1949).

Lameness resulting from skeletal abnormalities such as fracture of the *os pedis* is, in cattle, the most noticeable and economically important symptom, and it is usually this which draws attention to the disorder. Characteristic postures and type of lameness are observed and include crossing of the forelegs, the placing of the affected foot in the manger and a 'cat-on-hot-bricks' walk.

Loss of production is frequently alleged by farmers in fluorosis districts, but it is often difficult to evaluate how much of this is due to fluorine. In industrial districts other contaminants may have an

adverse effect on pasture quality, copper deficiency is known to be common (Burns and Allcroft unpublished data) and husbandry standards may not be high However, lameness can cause much loss of production and survey data indicate that primary systemic fluorine toxicosis is likely to occur only at the highest levels of contamination

Diagnosis is usually based on the characteristic lameness the presence of dental lesions in home-bred animals, the proximity to an industrial source of fluorine, and chemical analysis of urine, herbage and bone samples where possible The fluorine accumulation in bone is relatively little affected by the variations of contamination which may result in temporary low values in herbage and urine Where loss of production is likely to be involved blood or liver samples should be checked for possible copper deficiency

Differential diagnosis consists mainly of the elimination of other types of lameness, most of which have their characteristic appearance whereas in fluorosis cases there are usually no clinically observable lesions Exostoses are not directly related to the severity of the lameness and many animals with fractures of the *os pedis* show no palpable exostoses

Post-mortem examination, which does not provide any specific evidence other than confirmation of the dental and skeletal abnormalities should include an inspection for fracture of the *os pedis*

Control measures so far investigated have provided only partly satisfactory solutions Trapping of the fluorine in the chimney effluent is possible but seldom practicable in the case of large furnaces such as brick or steel works, because of the large volume of gas involved and the amount of water which would be required Some small furnaces have been successfully fitted with gas-trapping apparatus All such apparatus, however, reqoures adequate maintenance and operation

In rats the feeding of materials such as aluminium and calcium compounds which combine with fluorine to form relatively insoluble products has reduced fluorine absorption by about 50 per cent as measured by reduction in bone fluorine accumulation In cattle, however, aluminium compounds reduced bone accumulation by only 30 per cent in stalled animals (Hobbs *et al*, 1954) and 20 per cent in a commercial dairy herd (Allcroft and Burns unpublished data) whereas no reduction was observed in store cattle at grass (Boddie, 1960) This degree of alleviation merely delays rather than prevents fluorine accumulation reaching a damaging level

It has been apparent from survey and experimental evidence that losses can be substantially reduced by appropriate husbandry methods. The housing of even acutely and severely lame animals for several weeks usually brings about recovery, although it will be appreciated that it is upsetting to the farm economy if cows must be housed in summer when grass is growing rapidly. A good standard of nutrition and hygiene is of the greatest importance because the damaging effects of fluorine are greater in animals on a sub-standard level of nutrition or suffering from other inter-current disorders and in this context grassland management, which often presents special difficulties in industrial disticts, merits particular attention.

OTHER INDUSTRIAL CONTAMINANTS

A condition in cattle somewhat resembling the conditioned copper deficiency of 'teart' pastures and associated with molybdenum contamination of herbage near metal alloy works has been described (Buxton and Allcroft, 1955; Parker and Rose, 1955). Symptoms included scouring and loss of condition and decrease in milk yield. Blood copper levels were low and herbage analyses showed high molybdenum and fairly high copper levels. Satisfactory treatment. and control was obtained by copper supplementation.

Pastures are sometimes heavily contaminated with zinc dust. Damage to herbage can be severe, but the high tolerance of grazing animals to ingested zinc renders it unlikely that poisoning would occur.

In the vicinity of cement and lime works, diarrhoea and loss of condition have occurred in animals grazing dust-contaminated pastures. No toxic substances have been demonstrated in the dust, and it appears that the diarrhoea is the result of mechanical irritation. Recovery is usually rapid following removal from the contaminated pasture.

THE ECOLOGY OF THE GRAZING ANIMAL

Tansley (1939) has described a pasture as a biotic climax. Pasture research workers have always been strongly conscious of the importance of applying ecological principles in the agronomic context. The dynamic condition of a sward, with its sensitivity to climatic and biotic factors, has made the pasture manager realize that only by a most careful manipulation or compensatory adjustment of those factors under his control can he obtain optimum production, and maximum

profitability. Indeed the agronomist has never been slow to stress the importance of the pasture/animal complex, even if he has more often implied the effect of the animal on the pasture rather than the reverse (Davies, 1958). Although the purpose of the present book is to consider the effect of the pasture on the animal it should be stated at the outset that the grazing animal is but one of the factors in a complex ecological system. Even if it is considered that the grazing animal is the focus of this system, a variety of other separate, but interacting factors must be taken into account by workers in this field.

For example, it is now known that the productivity of grazing animals as well as of plants, is influenced markedly by climatic factors such as light and temperature. The most obvious examples of this are found in the field of reproductive physiology where it has been established in ewes of many breeds that sexual activity is influenced markedly by a change in the day length (Yeates, 1949, Watson, 1952, Hafez, 1952). Photoperiodism can also provide a stimulus for changing sexual activity in rams (Moule, 1950). Similarly, changes in temperature have marked influence on the reproductive efficiency of ewes (Dutt and Bush, 1955) and of rams (Phillips and Mackenzie, 1934). The accumulated effects of such physiological changes as these were studied in the field by Phillips and co-workers who were able to demonstrate clearly how climatic factors stratified livestock production in west and north Wales (Phillips and Davies 1949, Phillips, Davies and Brown, 1949). McMeekan (1952) has shown that a similar ecological stratification of the livestock industries exists in New Zealand, and Whyte (1960) has done the same for arid and semi arid areas of the world. The Welsh workers extended their observations on climatic and seasonal influences to a variety of topics, and showed that in addition to reproductive activity, growth rate, milk production, and herd wastage due to both disease and low productivity, were all significantly altered by temperature, altitude and/or day length (Phillips, 1946). The relative importance of each particular factor contributing to a climatic environment is difficult to assess and until further results from controlled experimentation in climatological chambers are forthcoming field observations will be incapable of accurate interpretation.

No doubt the physiological effects of climate on production and reproduction are primarily responses of the endocrine system to external stimuli. For example, the response of the thyroid gland to temperature and season has been clearly demonstrated (Bogart and

Mayer, 1946; Henneman, Reineke and Griffin, 1955). Less obvious physiological responses may nevertheless be important, as in the case of the bacterial population of the rumen which, according to Underwood and Moir (1956), varies in numbers with day length.

In addition to climate a further ecological factor which influences the health and productivity of grazing domestic stock is the activity of wild animals and birds. In certain parts of the world, e.g. areas in East and Central Africa, the yearly production of meat per acre is said to be higher from wild animals than it is from domestic ones. Much attention is now being paid to methods of conserving the indigenous fauna and of increasing its productivity. Research teams in Kenya (Hungate, Phillips, Hungate & MacGregor, 1960; Phillips, 1960) and in Australia (C.S.I.R.O., 1961) have recently demonstrated that *Bos indicus* cattle are more efficient in digesting poor quality herbage, and in conserving nitrogen, than are *Bos taurus*. In Kenya, Ledger *et al.* (1961) have also compared the carcass composition of a variety of wild ruminants, such as certain gazelle, the wildebeeste, and the oryx, with that of domesticated cattle. Their evidence suggests that the wild animals are much better adapted to a poor quality roughage diet and, in particular, are much more efficient in utilizing and conserving nitrogen than are domesticated cattle of either *Bos indicus* or *Bos taurus* species. A knowledge of the physiological mechanisms which account for these differences could lead to exciting advances in pasture use in those areas of the world such as Central and East Africa and Australia, where production is first limited by a deficiency of nitrogen rather than energy. In most areas of the world, however, wild animals and birds are of interest to those working in the field of animal production because of their competitive ecological importance rather than their intrinsic value as food producers. They may be of importance either in the direct competition for food, or in the part they play in disease dissemination.

Important examples of animals which compete for food with grazing domestic stock range from the caterpillar to the deer, the swan and the kangaroo. However, in view of the depredations that it has caused in many parts of the world, notably Australia, New Zealand and Britain, the European rabbit has frequently been cast as the most serious competitor of domestic stock for food. Information on the damage done by rabbits has been reviewed by Thompson and Worden (1956). The now well-known story of how the virus disease myxomatosis has been used to control the rabbit population during the lasr decade is an

excellent example of the manner in which a knowledge of ecology may be applied in order to increase food production. This example also illustrates well the limitations of this type of approach.

McDiarmid (1961) has recently given an account of some of the causes of morbidity and mortality in free-living wild life, and has discussed the possibility of wild mammals and birds acting as reservoir hosts for a variety of infections communicable directly or indirectly to domestic stock. Many examples can be cited of disease outbreaks in farm animals in which the infective agent has been carried by wild animals. For example, McDiarmid (1960) has pointed out that bovine tuberculosis may be carried by wild pigs, deer or rats and the possibility of migratory birds bringing foot-and-mouth disease to Britain has been discussed by Wilson and Matheson (1952). Recent papers (Thompson, 1961, Swain, 1961) have emphasized that as more land is cultivated or farmed particularly in the now undeveloped parts of the world, the disruption to present ecological systems may result in a heavy mortality in both indigenous and exotic species of livestock. Present knowledge of diseases of free-living wild animals has been reviewed by McDiarmid (1960) and it is to be hoped that in the future greater attention will be given to this subject. In the past, experience with diseases of humans such as malaria and yellow fever has perhaps led to too great a preoccupation with arthropod vectors and their control to the exclusion of a proper appreciation of the natural reservoir of infection in wild vertebrate hosts.

GENERAL OBSERVATIONS

It has frequently been claimed that the spread of improved methods of pasture establishment and management has been accompanied by the introduction and extension of a miscellany of ailments among grazing stock. Those concerned with animal health and production have often pointed an accusing finger at the plant breeder and agronomist and claimed that by their work they have created many new, or intensified many old problems of animal health. Examples to support this argument are easy to find. The increased use of nitrogenous fertilizer in temperate climates has been shown to increase the incidence of hypomagnesaemia. Throughout the southern half of Australia, pasture improvement has been based upon the introduction of subterranean clover, with subsequent problems of infertility in the grazing stock due to the high oestrogenic content of the sward. These are

but two examples of many which may be cited. The flaw to this argument is that it ignores the enormous increases in the productivity of livestock that concurrently have resulted from the work of the pasture scientists and which much more than offset the new hazards to animal health. Moreover, in some cases, the so-called 'new diseases' of grazing stock are old ones which have been revealed only recently by new and better methods of diagnosis, or have been complicated by physiological stresses which are the inevitable accompaniment of modern techniques of animal husbandry. For example, it is pointed out in Chapter 24 that the increased incidence of hypomagnesaemia is in part due to the fact that as a result of improved techniques the longevity of grazing animals has been increased, and age is a stress which makes animals more susceptible.

Nevertheless there still remains an essential truth in the statement that the pasture scientist has too frequently ignored the requirements of the grazing animal. However, to say this as an intended criticism of pasture scientists is to miss the point completely. The difficulty in the past has been that no one has been able to define the requirements of the grazing animal in terms intelligible to the plant geneticist, biochemist or physiologist. The inadequacy of expressing these requirements in terms of dry matter availability per acre, or in crude protein percentages, has long been obvious, but satisfactory substitutes have not yet been forthcoming.

Perhaps the most important advance made in the work on grazing animals during the last decade has been the move towards a definition of animal requirements in terms that are meaningful to both the animal scientist and the plant scientist. An excellent example of the progress made in this respect is given by the work of three teams of workers headed by Dr K. L. Blaxter at the Hannah Dairy Research Institute, Ayr, Mr W. F. Raymond at the Grassland Research Institute, Hurley, and Dr C. C. Balch and Dr J. A. F. Rook at the National Institute for Research in Dairying, Reading.

Blaxter and his colleagues have shown (see, e.g. Blaxter, 1960; Armstrong, 1960) that the range of net conversion efficiencies of metabolizable energy to body fat is due to the effects of different diets on rumen fermentation processes and, in particular, on the proportions of volatile fatty acids (V.F.A.), lactic acid and hexose which are absorbed by the ruminant. It has been shown that the number of K cal of fat synthesized per 100 K cal of V.F.A. dissimilated is in the order of acetic acid $<$ propionic acid $<$ butyric acid $<$ lactic acid $<$ glucose.

Balch and Rook (see e g , Balch, 1960, Rook, 1959) have similarly stressed the importance of the nature of the rumen fermentation processes in relation to the resultant V F A mixture, and have shown that individual fatty acids have both specific and general roles in metabolism Acetate has a general effect on the synthesis of all milk constituents, acetate and propionate have specific effects on milk fat synthesis, and propionate has a specific effect on the synthesis of the solids-not-fat fraction In Raymond's Department, V F A production has been measured in rumen liquor taken from sheep fed a variety of single herbage species (Tilley, Deriaz and Terry, 1960). It was found that acetic propionic acid ratios varied widely with the species of plant eaten, and that, in general, herbages of a high water-soluble carbohydrate content gave higher proportions of propionic acid

It is still too early to say with certainty what the ultimate conclusions from these various studies will be However, it appears that a new method of assessing the value of pasture plants for the growth or lactation of the grazing animal is now emerging No one would claim that a method based upon the V F A production from herbage could be comprehensive in its nutritional significance, but as a criterion of energy value it is certainly promising Moreover, if the animals' requirements can be interpreted in such terms as these, they can then be made intelligible to the plant scientist Already it has been suggested (Davies, 1960) that plant genotypes differ significantly in their contents of soluble sugars If this is a heritable character it may mean that for almost the first time the plant breeder will be able to select, at the request of the animal physiologist, for a physiological character in his plants There are signs that similar progress is being made in other directions and that the days of plant selection based exclusively on considerations of plant morphology, leafiness and the like are numbered Butler and Johns (1961) have reported that genetic differences in herbage levels of nitrate, iodine and the alkaloid perloline are tenfold or greater in ryegrass parent plants and smaller, but highly significant differences occur for a number of other constituents of nutritional importance to the grazing animal The work being done by the Plant Chemistry and Grasslands Divisions of the New Zealand Department of Scientific and Industrial Research is another excellent example of how the chemical constituents of a species of plant may be influenced genetically, and how the chemical composition may in turn determine the health and productivity of the animal

In his definition of the disease and production problems of grazing animals the animal scientist, whatever his discipline, is rapidly becoming more exacting in his standards of research. Progress since 1946 has been substantial but much remains to be done. It is hoped that this book will assist and stimulate all those who are concerned with the further advancement of our knowledge of the grazing animal.

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CHAPTER TWO

Grassland Management

D S MACLUSKY AND W HOLMES

Factors affecting grass production—Climate—Soil—Influence of season on growth and quality of grass—Herbage species—Effect of frequency and severity of defoliation—Irrigation—Value of clover—Fertilizer nitrogen—Effect on botanical composition—Effect on yield of grass-clover swards—Effects of phosphate and potash—Effects of faeces and urine—Mineral and trace element content of herbage—Manurial requirements—Importance of efficient utilization—Rotational or paddock grazing—Close-folding strip or fold grazing—Soilage, zero-pasture or mechanical grazing—Factors affecting amount of herbage consumed by the animal—Relative production per animal and per acre—Effect of supplementary feed on production per animal—Mechanical treatment of pastures—Harrowing—Trimming—Gang mowing—Conservation and grassland management—Methods of conservation—Hay—Dried grass—Silage—Relative importance and usage of conservation—Utilization of conserved grass feeds in livestock rations—Economics of grass production—Increasing grass production—Utilization of the extra grass

The efficient utilization of grassland is one of the most complex problems of agriculture Unlike most other agricultural crops, grassland is not always directly harvested and it is seldom possible to measure its yields with precision Moreover, the extent to which its potential yield is utilized does not depend simply on the farmer's ability to grow good crops but also on his skill in providing herbage, either fresh or in some conserved form, of a quality suited to the needs of the animals to which it is fed, and on his skill in animal husbandry Indeed grassland management can only be discussed as a combination of good crop and animal management In this chapter, however, it is

convenient and logical to consider the production of grassland in the first place and then to discuss the means by which this production may be utilized.

The factors affecting grass production which will be discussed here include climate, soil, plant species and strains, as well as the more strictly managerial factors including the use of irrigation and of fertilizers, the role of clover, and the effects of frequency and severity of defoliation. The sowing and establishment of grassland are outside the scope of this chapter. For these the reader is referred to Stapledon (1939) and the Imperial Bureau of Pastures and Field Crops (1945).

CLIMATE

Although grassland of various types is found in countries of temperate and tropical climate throughout the world, its productivity even within the confines of Britain is closely related to local and seasonal variations in weather conditions. Temperature, precipitation and the incidence of sunshine are important, not only for their effects on the annual yield of herbage, but especially for their effects on the duration of the growing period and on variations in growth rates and quality during the growing period.

Growth is critically influenced by temperature and does not start in the spring until the soil temperature exceeds 42° F. (Blackman, 1936). The growth rate then increases with increasing soil and air temperatures, but it may not continue to increase in direct proportion to temperature. For example, Mitchell (1954, 1955) found no response to increasing temperatures within the range of 59–83° F. Julen (1952), on the other hand, claimed that the growth rate increased with increasing temperatures and daily duration of sunshine except when the water supply was inadequate. Without an adequate water supply high temperatures depress the growth rate.

The water supply to the plant is, of course, not related solely to the rainfall but to the water balance of the soil. This is the sum of water available at the beginning of the season plus rainfall, less losses from drainage, run-off, evaporation and transpiration. Drainage is negligible in British summer conditions and the main loss is through evapo-transpiration which is governed by humidity, temperature, wind-velocity and the daily duration of direct sunshine (Penman, 1951). If the water supply is insufficient to maintain evapo-transpiration, growth suffers and ultimately wilting occurs. The magnitude of the losses through evapo-transpiration is indicated by estimates made at Rothamsted

which showed that in hot summer weather the moisture loss was equivalent to a rainfall of 0 25 in daily (see Russell, 1952)

The frequency and extent of moisture deficit in Britain have been calculated and it has been shown that long periods of moisture deficit occur in most years in the south and east of this country and are not infrequent even in the north and west in lowland districts (Ryall, 1952). The potential value of irrigation is, therefore, not limited to so-called dry climates and its effects will be discussed later

SOIL

The soil acts not only as a source of nutrients but as medium for plant growth Although different soils may be inherently rich or poor in plant nutrients their fertility is dependent also on their texture or physical condition i e their porosity, degree of flocculation and organic matter and humus content In this wide sense the texture of a soil affects its moisture-holding capacity, its ability to warm rapidly in the spring and also the rate at which its plant nutrients are made available to the plant (see Russell, 1952)

Grass can be grown on most soils, indeed one of the virtues of the ley or temporary grass sward is the way in which it improves the structure of both light and heavy soils (Stapledon and Davies, 1948, Davies, 1952) Light, well-aerated soils which readily become warm are among the earliest and most satisfactory of soils for grassland growth provided they are not subject to summer drought, although for the same reasons they are valuable for arable cropping On the other hand, heavy clay soils with poor aeration which are often unsuitable for tillage can be effectively utilized under grass They retain moisture in a dry season but because of their high moisture content they are slow to warm in the spring and consequently are late in growth. They may also show poor responses to fertilizer treatment In an experiment in Ayrshire, for example, a late heavy clay soil consistently showed yields of herbage only 70-80 per cent of those obtained on lighter soils at various comparable levels of manuring

THE INFLUENCE OF SEASON ON THE GROWTH AND QUALITY OF GRASS

With perennial grasses and clovers there is an annual phase of floral reproduction which is initiated in response to increasing day lengths and temperatures in the early spring (Cooper, 1950) From about a month later the energies of the plant are diverted from leaf production

to the growth of flowering shoots. The ratio of leaf to stem falls rapidly and with it the feeding value of the herbage. This is because the stem is higher in fibre content, and lower in crude protein content than the leaf (Fagan and Evans, 1926) and because it becomes increasingly lignified and indigestible as it matures (Norman, 1936). The crude protein content of the leaf also declines with maturity. The relation between leaf:stem ratio and herbage composition has recently been clearly shown by Waite and Sastry (1949).

Under good management, grass is allowed to mature in this way only when hay is made, but even with swards which are repeatedly cut or grazed the combined effects of the floral reproductive phase and of the weather result in marked seasonal variations in the yield and composition of herbage. In particular, herbage tends to become stemmy and low in protein content in May and June and to become leafier and higher in protein content in late summer and early autumn. Typical seasonal variations in the yield and quality of grass clover swards cut at regular intervals are shown in Fig. 2.1. The growth rate rises to a peak when flowering starts but during the period of reproductive growth the quality of the herbage declines. Dry conditions or a lack of plant nutrients may depress the yield and also the quality of herbage at this time. The vegetative phase resumes after June. If weather permits, the rate of growth may rise again, but it will not reach the maximum rate found in early summer.

HERBAGE SPECIES

Although many species of grasses, clover and other legumes are found in grassland, productive lowland grassland in Britain consists primarily of one or several of the following vigorous species: Italian ryegrass (*Lolium italicum*); perennial ryegrass (*Lolium perenne*); cocksfoot (*Dactylis glomerata*); timothy (*Phleum pratense*); meadow-fescue (*Festuca pratensis*); rough-stalked meadow grass (*Poa trivialis*); and smooth-stalked meadow grass (*Poa pratensis*). Tall fescue (*Festuca elatior*) is also occasionally sown. Several invading species are normally found in association with the sown species but they only form a large proportion of the sward where management or soil conditions are unsatisfactory: these include, notably, agrostis species (e.g. *Agrostis tenuis*; *Agrostis stolonifera*); annual meadow grass (*Poa annua*); Yorkshire fog (*Holcus lanatus*); sweet vernal (*Anthoxanthum odoratum*); crested dogstail (*Cynosurus cristatus*) and red fescue (*Festuca rubra*). These grasses are of low productivity and have a short annual period of growth.

A considerable amount of work has been carried out in the last thirty years in the comparison of the more vigorous species and the selection and breeding of different strains within each species for various purposes, especially the development of leafy high-tillering persistent strains. Whether or not the genetic differences which have been developed show themselves in practical conditions, however, depends very much on the environment and management to which the grasses are subjected. In general, differences in annual yield either between the important sown species or between their different strains are relatively unimportant compared with differences in persistency, leafiness and the seasonal distribution of yield (Holmes and MacLusky, 1955*b*, Hunt, 1956). In ryegrasses, for example, differences in productivity between bred strains and commercial strains have been found to be slight in the first few years after sowing but the bred pasture strains are more leafy and persistent although as much as three weeks later in spring growth (Heddle, Dawson and Gregor, 1950, Kirkwood, Gilchrist and Thomson, 1954, Prendergast and Brady, 1955).

Of the leguminous plants sown in association with grass, only four, white clover (*Trifolium repens*) red clover (*Trifolium pratense*), Alsike clover (*Trifolium hybridum*) and lucerne (*Medicago sativa*) are important. White clover is almost invariably used for grazing purposes. Several bred strains of white clover are available which differ both in vigour of growth and persistency. Davis and Cooper (1953), for example, have shown substantial differences in persistency and annual production between Kent and S100 white clover on the one hand and a Dutch white clover on the other, when sown with the same ryegrass and grazed by sheep (see also Troughton 1955).

The early or late-flowering varieties of red clover may also be included in grazing swards but, because of their vigorous growth, short life and high bloat-producing propensities they are better used in swards intended primarily for cutting for hay or silage at least in the first harvest year. The same may be said of Alsike clover which is used to replace red clover on acid soils. Although lucerne is generally regarded as a special-purpose crop for conservation it may also be included in swards for grazing or cutting (Davies, Morgan and Davies, 1953). It has been the subject of a recent memoir (Grassland Research Institute Memoir, No 1, 1955).

THE EFFECT OF FREQUENCY AND SEVERITY OF DEFOLIATION

It is a generally accepted principle in grassland management that for

the most vigorous growth, grass should be alternately rested and defoliated. The frequency, duration and severity of each defoliation affect the yield and quality of the grass produced and the persistence of individual species of the sward. As the data in Table 2.1 show, the

TABLE 2.1. *The effect of different frequencies of cutting or grazing on the dry-matter yield and crude-protein content of grassland*

100 lb. dry matter per acre approx.

Cutting experiments	Approximate interval between cuts (weeks) 1	2	3	4	5
(1) Woodman *et al.* (1929)*	19·8	25·6	32·2	—	—
Crude protein content (in D.M.) %	24·7	23·5	21·1	20·2	—
(2) Hamblyn (1954)†	31·5	42·1	50·1	—	66·2
Grazing experiments	**No. of grazings in the season 10**	**6**	**5**	**4**	**—**
(3) Williams (1952)					
(*a*) No fertilizer	39·0	61·0	—	—	—
(*b*) 70 lb. N per acre	53·0	70·0	—	—	—
(*c*) 139 lb. ,, ,, ,,	56·0	65·0	—	—	—
(*d*) 278 lb. ,, ,, ,,	66·0	76·0	—	—	—
(4) Bosch (1956)	—	97·2	103·5	108·0	—

* The values for crude protein were derived from four separate years (Woodman *et al.* 1931).

† The values quoted here are averages for four years' application of each treatment on a New Zealand sward.

more frequent the defoliation, the lower is the yield of dry matter at each defoliation and for the season as a whole (Woodman *et al.*, 1931; Jones, L. I., 1933; Hamblyn, 1954; Williams, 1952; Bosch, 1956). However, the herbage at each defoliation is less mature, that is, leafier, higher in crude protein content and lower in fibre content. In practice a compromise must be found between yield and quality according to the class of grazing stock for which the herbage is produced or the method of conservation.

The effects of frequency of defoliation on yield appear from some of the results in Table 2.1 to be less pronounced in grazing than in cutting conditions, but this point requires investigation within one experiment since comparison between experiments in this way can be

misleading The relatively small increase shown by Bosch (in Table 2 1) may be due to the high general level of yields in his data, for Williams's (1952) results suggest that a reduction in the frequency of grazing gives a smaller increase in yields at high levels of fertility than at low levels

The effect on herbage yields of severity of defoliation (i e the level down to which grass is cut or grazed) has also not yet been fully examined It has been generally accepted that the greater the severity of each defoliation, the less is the yield of herbage in the season (Stapledon, 1924, Roberts and Hunt, 1936) This is because the removal of increasing amounts of leaf makes regrowth increasingly dependent on the plant's food reserves in the base of the stem or the root, rather than on photosynthesis Root development, however, is also reduced by close defoliation (Troughton, 1957) From studies with Italian or hybrid ryegrass and red clover swards, Brougham (1956) concluded that for the maximum herbage production per acre the amount of leaf remaining after defoliation should be sufficient to ensure complete light interception by the sward In this particular sward the optimal area of leaf for this purpose and the most rapid rate of recovery was achieved by cutting to 5 in rather than 3 or 1 in Similar general conclusions were reached by another New Zealand worker, Mitchell (1954) from detailed studies with single ryegrass plants and by Stewart and Hyde (1954) from grazing practice Reid (1959) at the Hannah Institute, however, found the opposite result In his experiments with established perennial ryegrass/white clover swards, repeated cutting by machine to 1 in as compared with 3 in over several seasons gave consistent increase in dry matter yield of 20–40 per cent, a result which was attributed to the removal of flower initials from the growing point and increased vigour of vegetative growth. This result was not confirmed when the comparison was repeated in rotational-grazing conditions on similar swards The difference between the results of the cutting and grazing experiments at the Hannah Institute may possibly be explained by the longer duration of the period of each defoliation in rotational grazing This allows the grazing animal to remove the early regrowth which probably depletes the plant's food reserves and delays recovery It appears from these results that close-grazing may improve output provided the grazing periods are of short duration and infrequent The contradiction between the results of different experiments, however, requires and is receiving further investigation at several centres

Grass species and strains differ in their ability to withstand close or frequent grazing. Perennial ryegrass, for example, can withstand frequent close grazing which would eliminate cocksfoot (Jones, M., 1933). The location of the plant's food reserves, whether in the root (in perennial ryegrass) or in the base of the stem (timothy and cocksfoot) and the effects of competition between plants (especially for light) are important factors affecting the vigour and persistence of individual strains or species in the sward under different systems of management. The classical experiments on the influence of grazing management on the botanical composition of a sward were those carried out by Martin Jones (1933) at Jealott's Hill. This work was substantiated later by L. I. Jones (1939) at Aberystwyth. These workers showed that as a general rule the defoliation of any one grass in the period when it was actively growing reduced its vigour and its ability to compete with other species later. To allow it to develop, on the other hand, strengthened its root system and increased its competitive power for water, nutrients and light. For example, repeated severe grazing of early-growing grasses in successive springs weakens them and allows clover and later grass species to develop. The poorer species of grass (*Agrostis* spp.; *Poa* spp.) do not reach maximum growth until early summer. Undergrazing at this time of year strengthens these especially if the better grasses have been weakened by hard grazing earlier in the season. If such treatment is repeated in successive seasons the sward degenerates until it is dominated by the poorer grasses.

These principles may be applied in a planned rotation of treatment designed to provide herbage for conservation or grazing at various times of the year without deterioration of the composition of the sward (Davies, 1952). An example is shown in Table 2.2 (Moore, 1943).

TABLE 2.2. *An example of rotation of treatment of grassland* (based on Moore, 1943)

Number of years after sowing	April	May	June	July	Aug.	Sept.
1	—	graze rotationally				rest
2	early bite	rest	cut for silage			
3	hard grazing throughout the season to encourage clover					
4	—	—	hay		aftermath grazing	

IRRIGATION

From what has been said earlier on water deficit and its effects on seasonal variation on the growth of grassland, it will be appreciated that in most years irrigation may be expected to increase the production of grassland not only in the south-east where the water deficit is most acute, but in most lowland districts in Britain.

Increases in yield from irrigation in the south-east of Britain have been substantial in dry seasons, but small in wet seasons For example, Schofield (1952, 1953) reported that in 1953 the provision of 5 in. per acre of water raised the yield of grass at Rothamsted from 68 to 98 cwt of dry matter per acre, but that in 1952, a wet season, the same amount of water increased yields from only 82 to 92 cwt. per acre. The effects of irrigation on the yield of pastures have also been studied over many years at the Jealott's Hill Research Station in the Thames valley, where the rainfall averages 28 in. a year. Between 1932 and 1951 an average application of 6·7 in. of water per acre in each season increased the yield on average by about 1 ton of dry matter per acre, that is, 3 cwt. of dry matter per acre per in. of water (Lewis, 1952). Obviously, therefore, irrigation offers possibilities of striking increases in the output of grassland and the only important deterrents to its widespread use could be cost or difficulty in procuring a supply of water.

In the past, sprinkler irrigation has been limited to certain arable and horticultural crops from which monetary returns were higher than those expected from grassland. The cost of irrigation however, is not unduly high, and a higher cost of pasturage than usual would be justified if herbage growth were otherwise so depressed by water shortage that the feeding of conserved and concentrated feeds had to be resorted to.

The cost of an inch per acre of water over the years 1931–51 has been given by Lewis (1952) as £2·75. Fell (1951) has given a similar figure, £2·85, and more recently Wright (1956) has estimated the cost as only £1·5 per acre per in. The cost of the herbage produced is, therefore, at the most about 18s per cwt. of dry matter which cannot be regarded as high if the alternative is the feeding of conserved products or concentrates.

Because the first effect of water shortage in almost any crop is to restrict the production of leaf (Russell, 1952), irrigation generally results in an improvement in the quality of herbage as well as in yield. Part of this improvement is attributable to the invigoration of clover (Robinson, Sprague and Lueck, 1952). Irrigation increases the mineral

content of grass, and the succulence of irrigated herbage ensures its palatability to grazing stock.

Wind (1954) has shown that moisture loss through evapo-transpiration is not increased when yield is increased by the use of nitrogen fertilizer. The use of irrigation together with nitrogen fertilizer, therefore, increases the efficiency with which both the water and the fertilizers are used.

THE VALUE OF CLOVER

The main natural source of nitrogen to the grass crop is clover. That atmospheric nitrogen is fixed by clover-root nodule bacteria is, of course, well known, but the mode of transference of this nitrogen to the grass has been the subject of controversy for some time. It appears that in farming practice the most important mode of transference is through the grazing animal (see Melville and Sears, 1953; Walker, Orchiston and Adams, 1954; Walker, 1956).

The contribution of clover to the nitrogen requirements of grasses and to the productivity of the sward as a whole is governed by the vigour of the clover strains present, by climate and by management. Estimates of the amount of nitrogen made available yearly from this source range from 175 lb. per acre in this country (Holmes and MacLusky, 1955*b*) to as much as 600 lb. per acre in New Zealand (Walker, 1956). Obviously clover as a source of nitrogen should not be neglected and one of the major economic questions in grassland management is the extent to which the legume can be relied on as a source of nitrogen and in what circumstances it should be supplemented or replaced by fertilizer nitrogen.

The grass-legume association suffers from at least three disadvantages. First, growth may be slower in the spring than with fertilizer nitrogen (Blackman, 1936). Second, the production obtainable from the grass-clover sward is often lower than that obtainable with the application of nitrogenous fertilizer. Third, the incidence of bloat in cattle is often closely associated with a high legume content in the sward.

In practice, economic and climatic factors influence the relative use of the two sources of nitrogen. In New Zealand where fertilizer costs are high and climatic conditions favourable to clover, fertilizer nitrogen is rarely used. In the Netherlands, on the other hand, where fertilizers are cheap, heavy use is made of nitrogenous fertilizer. In Britain liberal amounts of fertilizer nitrogen are used on some farms, particularly those engaged in producing grass for artificial drying or

small farms where high output per acre is essential, but a compromise is more common in which both sources of nitrogen are used

FERTILIZER NITROGEN

Provided that the mineral supply, moisture supply and soil temperature are adequate the yield of grass is extremely sensitive to fertilizer nitrogen Grass is indeed more responsive to high levels of nitrogen manuring than most other crops (Yates and Boyd, 1949) and the efficiency with which it converts nitrogen to plant material is relatively high

The main factors governing the response to nitrogen are the frequency of defoliation, the timing and level of application, weather conditions and the species of grass Where clover is making a substantial contribution to the yield of grassland, the effects of nitrogenous fertilizer which are described below may be reduced

The increase in yield of herbage per unit of nitrogen applied is greatest when the sward is cut least frequently For this reason the increment per unit of nitrogen is greater for hay crops than for pastures or for swards cut regularly for conservation A recent survey by Boyd and Lessels (1954) showed that with an average application to hay crops of about 20 lb N per acre there was an average increase in yield of about 35 lb dry matter per lb N applied, whereas in silage and grass-drying experiments receiving an average application of 50 lb N per acre there was an increase in yield of only 20 lb dry matter per lb N applied The smaller response of the silage and dried-grass swards is unlikely to have been attributable to the fact that a greater total amount of nitrogen was applied in the season

The data quoted by Mulder (1952) from work in the Netherlands show little evidence of diminishing response to fertilizer nitrogen with applications of up to about 180 lb N per acre per annum Evidence obtained at the Hannah Institute is in agreement with this (Holmes and MacLusky, 1955*a*), although in the latter experiment there was a slight reduction in yield of dry matter per lb nitrogen applied when more than 50 lb per acre were applied at one dressing There was no diminishing response in crude protein yield with applications of 104 lb N per acre at each dressing

It is probable that responses lower than these may be found in drier climates Boyd and Lessels show that hay increased in yield by over 40 lb dry matter per lb N application in Scotland, Wales and south-west England, and by about 30 lb in the south-east Regional dif-

ferences are not available for swards cut repeatedly during the season, but the general level of response to heavy applications of nitrogen quoted for such swards by Boyd and Lessels was similar to responses found at the Hannah Institute in Ayrshire when a sward containing clover was used as control (Table 2.3).

TABLE 2.3. *The response of dry matter per pound fertilizer nitrogen applied to swards for silage or artificial drying*

Fertilizer nitrogen (lb. per acre)	Response of dry matter per lb. N applied	
	Boyd and Lessels survey of 40 experiments in the United Kingdom	Hannah Institute in Ayrshire
34–67	20	—
78–179	16	20
190–336	12	17

There appears to be no great variation between different parts of the country in the efficiency of nitrogen recovery as distinct from the dry-matter yield response. The effect of fertilizer nitrogen on the vigour of the clover is of more importance than regional differences in affecting the net return from fertilizer nitrogen. Between 40 and 70 per cent of the nitrogen applied may be recovered on pure grass swards but on clover–grass swards the suppression of clover by fertilizer nitrogen may result in a net recovery of only 0–40 per cent. (This is discussed in greater detail on page 43.) Since even in the best conditions 30 per cent of the nitrogen applied is not recovered in the crop, the fate of fertilizer nitrogen on and in the soil invites further study.

The efficiency of nitrogen utilization and the dry-matter yield response have been shown to be highest in the spring (Holmes, 1949) but this is governed by the earliness of the grass. Early-flowering strains show high recoveries and late-flowering strains low recoveries of nitrogen in the early spring (Holmes and MacLusky, 1955*b*). In midsummer the efficiency of nitrogen utilization may be reduced by drought, but some of the nitrogen applied may be utilized at a later date. In the autumn, of course, the efficiency of utilization declines because of declining temperatures and day lengths. However, even in the south-east of the country, nitrogenous manuring results in a more

uniform growth curve during the season and improved production in in the second half of the season (Watson, Procter and Ferguson, 1932)

Different species of grass may show differences in efficiency of nitrogen utilization A recent comparison of several common species and strains of grasses grown without clover showed that when nitrogen was applied, while all the grasses had similar crude protein contents, cocksfoot gave the greatest increase in yields of dry matter and crude protein, followed by timothy and, lastly, ryegrass There were no consistent differences between strains within species, except as already mentioned in seasonal variations in response to nitrogen (Holmes and MacLusky, 1955*b*)

No consistent differences in efficiency have been found between the nitrogenous fertilizers in common use in this country provided they are applied in quantities which supply similar amounts of nitrogen Nitrogen in the form of nitrate (NO_3), however, is slightly quicker acting than in the form of ammonium (NH_4) There is a loss of 1½ lb calcium carbonate from the soil for each lb of sulphate of ammonia applied (Lewis, 1938), but this can be remedied by liming or prevented by the use of a neutral nitrogenous fertilizer

THE EFFECT OF FERTILIZER NITROGEN ON BOTANICAL COMPOSITION

Regular dressings of nitrogen produce a rather open sward by increasing the size of individual grass plants There is a consequent reduction in the clover, the less vigorous grasses and weeds The proportion of the more vigorous grass species increases in the sward in proportion to the amount of nitrogen applied These effects are due to the rapidity of growth of the more vigorous grasses when nitrogen is applied and to the resultant shading of slower-growing species It has been suggested that the ammonium ion has a toxic effect on non-gramineae (Blackman, 1932) and that the suppression of clover in particular may be due to reduced fixation of nitrogen and to increased competition with the grasses for nitrogen and other nutrients, especially potash, for water and for light (Blaser and Brady, 1950) Recent results obtained at Wye College (Young, 1958) indicate that although the number of plants is reduced by shading from the grass when nitrogen is applied, the efficiency of nitrogen fixation by surviving clover plants is unimpaired

Two important weeds which are not suppressed by nitrogen are dock (*Rumex acetosella*) and couch-grass (*Agropyron repens*), both may

thrive under a system of regular cutting when heavy nitrogen dressings are applied. With the more flexible management applied to pastures, however, the problem is less serious.

THE EFFECT OF FERTILIZER NITROGEN ON THE YIELD OF GRASS–CLOVER SWARDS

Because clover is depressed by competition from the grasses when fertilizer nitrogen is applied, the net increase in dry-matter yield from the application of nitrogen is not so great on grass–clover swards as when it is applied to pure grass swards. In fact, an increase in yield from fertilizer nitrogen applied at one season or in one year may result in subsequent reduction in yield unless nitrogen applications continue (Holmes, 1951; Walker, Edwards, Cavell and Rose, 1952).

The suppression of clover increases with increasing amounts of nitrogen applied, and is greater the more advanced the herbage is allowed to become before it is defoliated (Walker, Edwards, Cavell and Rose, 1953). Therefore, where herbage is regularly fertilized with nitrogen and cut at a long leafy stage, the clover content of the sward is rapidly depressed, but where the grass is kept short under a system of continuous or frequent grazing, the use of nitrogen will not necessarily reduce the amount of clover present (Hamilton, 1950; Williams, 1952).

There are marked differences between different species and strains of grass in their compatibility with clover which are accentuated when nitrogen is applied regularly. The extent to which clover is depressed when nitrogen is applied depends on the time of application in relation to the growth rhythm of the companion grass and on its vigour and growth habit. In an experiment at the Hannah Institute, the results of which are summarized in Table 2.4, it was found that grasses which when grown alone were most responsive to nitrogen, yielded least when grown with clover and gave small responses to regular dressings of nitrogen when grown with clover. For example, some cocksfoot strains suppressed the clover more and yielded less when grown with clover than did timothy or ryegrass. The effect of nitrogen was to accentuate these differences in compatibility. The time of application appeared to be important in this respect. The greatest depression in clover content occurred as a result of the spring application especially with ryegrass. These effects may not be found under grazing conditions if the stocking intensity is adjusted to keep pace with the growth of the grass.

TABLE 2.4 *Dry-matter yields (100 lb per acre) of various strains and species grown alone and grown with clover or fertilizer nitrogen or both*

Species and strain	Grown without clover	Grown with clover	Grown without clover + 10 cwt 'Nitro-Chalk'	Grown with clover + 20 cwt 'Nitro-Chalk'
Ryegrass S101	21	48	51	74
Ayrshire	21	52	51	70
Cocksfoot S26	21	33	74	65
Danish	25	49	73	79
Timothy S48	22	40	60	78
Scots	20	52	61	79
Meadow fescue S53	20	49	51	75

The depression of clover by nitrogen means that there may be little benefit to the total yield of herbage from small dressings of nitrogenous fertilizer (Watkin, 1954). Hamilton (1950), on the other hand, suggests that nitrogenous fertilizers can be applied at rates up to 900 lb 'Nitro-Chalk' per acre even when two cuts are taken for silage, without loss of clover, if the management is sufficiently skilful, and that there

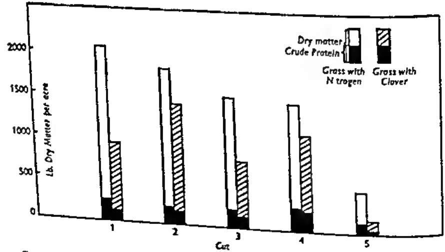

FIG 2.1 Seasonal variation in the dry-matter yield of S26 Cocksfoot grown with S100 clover and of the same grass without clover but treated with 2 cwt 'Nitro-Chalk' per cut.

is no difficulty in maintaining the clover at rates up to 450 lb. per acre. Much will depend on the species of grass in question.

The clover content is not always an index of the productivity of a sward. Williams (1952), for example, has shown that with a sward grazed 10 times in the year clover was maintained and a high recovery of fertilizer nitrogen obtained with applications of up to 278 lb. N per acre: but that with 6 grazings the yield of herbage dry matter was higher, although the clover content and the recovery of nitrogen were both depressed. It is important, therefore, that in attempting to encourage the growth of clover the frequency of grazing is not so high as to impair unduly the vigour of the grasses and so prevent them from benefiting by their association with clover.

The benefit of nitrogenous fertilizers may lie in the provision of herbage at times when it is required, rather than in any substantial increase in yield over the long term. The optimal times and rates of nitrogenous manuring for different swards and management methods which will allow the benefits of nitrogenous fertilizers to be gained without damaging the clover require further study.

THE EFFECTS OF PHOSPHATE AND POTASH

The importance of phosphate has been widely appreciated since its effects were demonstrated in early work at Cockle Park (Gilchrist, 1906; Somerville, 1924). In that work the value of phosphate lay in the invigoration of the clover in the sward. Phosphate also encourages a strong root system and for this reason generous dressings of phosphate are important in the successful establishment of grass–clover swards (Stewart, 1952).

Phosphatic fertilizers have been widely used on the better British grasslands in the past 20–30 years and it is probable that on many pastures continued heavy phosphate dressings are unnecessary. Lewis (1955) has recently commented on the lack of response of British grassland to phosphate; experiments at the Hannah Institute (Holmes and MacLusky, 1955*a*) showed no phosphate response until after six years of very intensive management; and Norman (1956) has shown that small dressings of superphosphate (37 lb. per acre) applied thrice in each season were as effective in maintaining grass production as heavier dressings although the latter increased the phosphorus content of the herbage. Moreover, it is now considered probable that a vigorously growing grass sward can release so-called fixed phosphate from the soil. For example, Stewart and Holmes (1953) using heavy nitrogen dressings

removed some 70 lb P_2O_5 per acre annually for four years from plots which had received no phosphate and which were on a soil with a high fixing capacity

It may be concluded, therefore, that on the better lands of Britain relatively light phosphate dressings applied frequently are adequate unless there is evidence of a low phosphate content in the herbage, when heavier applications will be beneficial On the other hand, there is a growing appreciation of the importance of potash in maintaining production from grassland This will be readily understood when it is considered that while the P_2O_5 content of grass dry matter is normally between 0 5 and 1 6 per cent, that of K_2O is between 2 and 5 per cent Where herbage is cut and removed, therefore, the amount of potash returned has a crucial effect on the yield and botanical composition of the sward (see also Melville and Sears, 1953)

Table 2 5 summarizes the first six years' results of an experiment at the Hannah Institute in which a predominantly ryegrass sward was

TABLE 2.5 *Average yields over six years (in 100 lb per acre) dry matter of a mixed sward with and without nitrogen, phosphate and potash*

(The nitrogen dressing was 520 lb N per acre split over four or five cuts in the season)

Treatment	1947	1948	1949	1950	1951	1952	Mean
Without nitrogen							
No minerals	53	51	37	33	36	47	43
Phosphate	46	37	31	35	35	37	37
Potash	35	39	38	35	44	52	40
Phosphate and potash	51	53	47	49	71	59	55
With nitrogen							
No minerals	86	53	43	37	38	48	51
Phosphate	92	61	51	38	38	38	53
Potash	99	88	92	93	100	106	96
Phosphate and potash	81	81	97	94	108	116	96

given massive dressings of nitrogen with and without phosphate and potash. When heavy applications of nitrogen were made without potash there was a rapid decline in yield from year to year The proportion of vigorous grasses declined and these were replaced by indigenous species, especially *Festuca rubra* and *Agrostis* spp which probably because of their superior cation exchange capacity (Drake,

Vengris and Colby, 1951) are able to survive although at a low level of yield, in soils depleted of potash. When neither nitrogen nor potash was applied the same deterioration occurred in the sward but at a much slower rate. Where adequate potash was given a big response to nitrogen was obtained and yields were maintained or even increased over a period of ten years with a gradual increase in the proportion of vigorous grasses (mainly ryegrass and timothy). This incidentally resulted in earlier growth each season.

The importance of potash for the maintenance of a vigorous stand of clover has been shown by Blaser and Brady (1950) in America. These authors found that dressings of 150 lb. K_2O per acre in the year increased the amount of clover to two or three times the original amount in the sward whether or not annual dressings of 100 lb. N were given. It does not follow that heavy dressings of potash will maintain the clover content of a sward given heavy dressings of nitrogen and cut repeatedly. In these conditions clover is eliminated presumably because of shading by the grasses (Holmes and MacLusky, 1955*a*).

The effects of potash on the yield and botanical composition of pastures are not so pronounced as on grass cut for conservation because grazing animals return a large proportion of the phosphate and potash they consume. Unfortunately, there is scarcely any experimental evidence available on the potash requirements of pastures. Wherever herbage is cut for any form of conservation, however, and on pastures on dairy farms where so much potash is lost in byre drainage, the potash requirements of pastures are probably much higher than they are generally supposed to be.

THE EFFECTS OF FAECES AND URINE

The effects of the faeces and urine of grazing animals on the botanical and chemical composition, productivity and manurial requirements of grassland have recently been the subject of direct investigations by Sears and others in New Zealand (e.g. Sears and Newbold, 1942) and by Watkin (1954) in this country. These studies have been carried out using sheep, and the emphasis until recently has been on the nitrogen contribution of excreta rather than the mineral balance. It is to be hoped that similar studies will be carried out if possible using dairy cattle and that the mineral status of the soil will receive attention, since with dairy cattle the loss of plant nutrients is greater than with other classes of stock.

The effect of excrements on the sward is almost entirely explained by their contents of nitrogen and potash (Walker, Orchiston and Adams 1954, Mundy, 1961) Dairy cattle excrete in urine and dung about 70 per cent of the nitrogen, 63 per cent of the phosphorus, 86 per cent of the potassium and 65 per cent of the calcium they consume (Bear and Bender, 1948) The urine contains about 50 per cent of the nitrogen and 84 per cent of the potash excreted and these are both in readily available form Practically all the phosphate and the magnesium excreted are contained in a less readily available form in the faeces Since the palatability of herbage to dairy cows is increased by urine and reduced by faeces (MacLusky, 1960) the available nitrogen and potash but not the phosphorus or magnesium, utilized by the plant are consumed again and redistributed at each grazing Because the effect of urine on the growth of the pasture is more pronounced than that of faeces, the overall effect of excrements is to stimulate the growth of grass rather than of clover (Sears and Thurston, 1952)

The amount of nitrogen returned to the soil in an available form by dairy cows has been estimated by Walker Orchiston and Adams (1954) as 50–60 per cent of the nitrogen consumed Although not all the excreta are dropped by the cow while at pasture, this estimate agrees with the value of 0 5 lb nitrogen contributed per cow per day estimated by Holmes (1954*a*) In practical terms cows return the equivalent of 112 lb of nitrogenous fertilizer of 15–20 per cent N for each 30–40 grazing days spent on the pasture

The excretion of potassium may be calculated to be about 0 6–0 7 lb K_2O per cow per day In 30–40 cow-days per acre the cow will, therefore, excrete the equivalent of about 37 lb of 60 per cent muriate of potash Nevertheless in a grazing season of 200 grazing days, the probable deficit in the soil is equivalent to at least 56 lb muriate of potash per acre Not only is potash lost on roads and in cow sheds, but the possibility of fixation (Bray and De Turk, 1938) and of leaching (Pearson, 1952) of potassium must also be considered On the other hand, at Wye College, Wolton (1955) has shown that although sheep returned only 80 per cent of the potassium they consumed (of which 90 per cent was excreted in the urine) the soil reserves of available potash at the end of a year in which only urine was returned to the soil had increased by almost 30 per cent Since the soil reserves had declined when no excreta were returned, it appeared that in this experiment the sheep not only redistributed soil potassium but increased its availability

THE MINERAL AND TRACE ELEMENT CONTENT OF HERBAGE

The mineral content of herbage is related mainly to the content of available minerals in the soil. There is not normally any important difference in mineral content between different species or strains of the principal cultivated grasses, but these are richer in minerals than the less vigorous grasses such as *Festuca rubra* or *Nardus stricta* which are found on the poorer soils (Thomas, Thompson, Oyenuga and Armstrong, 1952). The values given in Table 2.6 may be taken as fairly typical for cultivated grassland herbage.

TABLE 2.6. *The decline in the mineral and trace element content of herbage with increasing maturity* (Thomas *et al*, 1952)

The values shown are contents in the dry matter.

Perennial ryegrass	Young leafy	Long leafy	Flowering	Mature
Calcium (% CaO)	0·94	0·84	0·51	0·50
Phosphorus (% P_2O_5)	0·69	0·72	0·57	0·57
Potassium (% K_2O)	2·78	2·71	2·36	2·32
Magnesium (p p.m. MgO)	0·51	0·34	0·27	0·41
Copper (p.p.m. Cu)	15·20	7·10	4·80	6·50
Cobalt (p.p m. Co)	—	0·17	0·15	0·14

There is, however, considerable variation in the mineral content of herbage according to the mineral status of the soil, manuring, stage of maturity and the season or climate (Deijs and Bosch, 1951).

When the mineral status of the soil is inadequate for the growth of the vigorous grass species these are replaced by less productive species (p. 46). If nutrient is scarce and therefore acting as a limiting factor to growth, further applications of a nutrient may result in 'luxury consumption' by the plant. As a general rule an increase in the concentration of one cation on the soil increases the concentration in the plant of that cation at the expense of others (Marshall, 1944).

Drought is reported to have little effect on the calcium content and to have irregular effects on potassium but it depresses the phosphorus content sharply (Ferguson, 1931), probably by reducing the availability of phosphate in the soil (Wolton, 1955).

The effect of nitrogenous fertilizers is to increase the content of calcium, magnesium and sodium in grass, but not generally the content of phosphorus or potassium. Although nitrogen increases the calcium

content of grasses, the depression of clover which occurs when nitrogen is applied to a grass–clover sward reduces the calcium content of the sward as a whole (Walker, *et al*, 1952) Stewart and Holmes (1953) found that the content of manganese and other trace elements was unaffected except for copper, whose content was markedly increased, but that these effects depend on the reserves of each nutrient in the soil On soil deficient in phosphorus, the effect of nitrogen may be to depress the concentration of phosphorus in the plant, while on soils rich in phosphorus nitrogen may increase it (Walker, *et al*, 1952) Hignett and Hignett (1951) have suggested that the ratio of Ca P_2O_5 in the diet may influence the fertility of cattle This ratio can to some extent be controlled by adjusting nitrogenous and phosphatic manuring Nitrogen applications reduce the clover, and therefore, the calcium content, while phosphate applications increase the phosphorus content of the herbage

The effect of potash fertilizers is to maintain the potash content in the plant when nitrogen is applied and to increase the potash content in the absence of nitrogen The increase in potash content is associated with a reduction in the content of sodium, magnesium, and possibly calcium (Stewart and Holmes 1953) The depression of magnesium may affect the incidence of hypomagnesaemia or grass-tetany in cattle

MANURIAL REQUIREMENTS

Traditionally the procedure on well-managed grassland has been to apply heavy dressings of 10–15 cwt basic slag when ploughing old pasture for re-seeding, and to apply phosphate every 3–4 years in amounts equivalent to 1 cwt superphosphate a year Most grassland, however, has until recently received very little fertilizer

In general the need for more frequent and more generous manurial treatment particularly with nitrogen and potash, has become better appreciated This is especially true in dairy farming where the loss of soil nutrients is greatest Manurial requirements are, of course, highest in swards cut continually for conservation In such conditions, fertilizers should be applied in amounts sufficient at least to replace the loss and a general rule is to apply 1 cwt of 80 per cent superphosphate and 1 cwt. 60 per cent muriate of potash per ton of dry matter removed This can be done by the use of compound fertilizers containing N, P_2O_5 and K_2O in the ratio of 12 4 12, or similar ratios Recent studies have indicated that for a period which will depend on the magnitude of soil reserves, lower replacement rates of P and K are

adequate to maintain herbage yield and these will reduce the likelihood of high potassium concentrations in the pasture herbage (Castle and Holmes, 1960).

At the other extreme with beef cattle or sheep when no excrements or herbage are removed from the field, annual dressings of 1–2 cwt. superphosphate and ½–1 cwt. of 60 per cent muriate of potash per acre are adequate to maintain fertility. On heavy soils rich in potash, smaller dressings of potash might suffice; on light sands, chalks or gravels, twice as much potash might be found necessary. These amounts should be increased in proportion to the amount of herbage removed for conservation.

The optimal rate per application for nitrogenous manures for pastures is 35–50 lb. N per acre, that is, 2–3 cwt. 'Nitro-Chalk' or 2–2½ cwt. sulphate of ammonia. Less than this may depress the clover and fail to produce any marked increase in yield. Higher rates up to 100 lb. N per acre are suitable for silage and dried-grass crops. With efficient grass management, and provided allowance is made for mineral requirements, there is no reason why such dressings should not be applied three, four or five times in the season.

THE UTILIZATION OF GRASS

THE IMPORTANCE OF EFFICIENT UTILIZATION

Although grassland is potentially one of the most productive crops, the quantity of feed actually utilized from grassland is on the whole extremely low. The fault often lies not in low productivity but in inefficient utilization, or in other words, bad grassland management. Although the average grass-clover sward can be expected in Britain to produce in a season at least 5,000 lb. of dry matter per acre, equivalent to about 3,000 lb. of starch equivalent, the average yield of utilized starch equivalent has been estimated to be as low as 1,100–1,300 lb. per acre (Hamilton, 1952). It is possible that this low output is an underestimate, because the system by which utilized starch equivalent output is normally estimated (Barker, Cray, Foot, Ivins, Jones and Williams, 1955) is subject to several errors to which grassland becomes the 'residuary legatee' (Cooper, 1954). But there is no doubt that utilized output of our grassland is low, that it compares unfavourably with some other countries and that it could be raised by better management.

An example of the loss in grass utilization in grazing was given in a

Swiss experiment by Grandjean (1937) On one half of a pasture the production of starch equivalent was estimated by cutting the herbage and by chemical analysis The yield of starch equivalent was twice that estimated to have been utilized by dairy cattle grazing the other half of the pasture Improvements in management in the subsequent year raised the utilized output to almost 75 per cent of the possible output Calculations of this sort are, of course, subject to serious errors, but the important point this experiment demonstrates is that a substantial increase in utilized output was gained simply by improving grazing management Similar results have been shown by Eyles, Williams and Green (1956) Attention has also been drawn to the same situation on New Zealand pastures where a total yield of 9 000 lb herbage dry matter per acre is readily obtained (McMeekan, 1952) Although such a yield should supply the nutrients for cows and the production of 600 lb butterfat per acre McMeekan pointed out that in practice yields of over 300 lb per acre are seldom achieved

GRAZING METHODS

Continuous grazing This is probably the most widespread grazing system in Britain The success of the system depends both on the intensity of stocking of the pasture and on the flexibility of stocking during the grazing season If the pasture is adequately stocked, the herbage is kept short and leafy, and there is little wastage, but with very heavy stocking the amount consumed daily by the animal may be inadequate for its needs and productivity of the sward will probably be depressed On the other hand, with very low stocking intensities, much of the herbage will be able to mature and grow coarse, and while the animals may thrive (because they will be able to select herbage of high feeding value) the utilized output of the pasture will be very low If as in 'set-stocking' the stocking rate remains constant throughout the season one or other (or both) of these extremes will occur If continuous grazing is to be successful, therefore, it is important that as the rate of herbage growth rises towards summer, the stocking intensity be increased so that the rate of consumption keeps pace with the rate of herbage growth and that similarly when the rate of herbage growth declines the stocking intensity be reduced. This can be done fairly readily on farms which are fattening lambs or finishing bullocks In experimental conditions using dairy cows a satisfactory utilized output has been achieved with continuous grazing when the stocking rate was carefully adjusted according to variations in herbage growth

(see p. 59). On commercial dairy farms, however, the number of stock is relatively constant and this adjustment of stocking intensity cannot usually be made unless a concession is made to the rotational system. It will be appreciated, of course, that additional grass is commonly available for stock after hay or silage has been produced from part of the farm and that in this way some additional pasture is nearly always made available in the second half of the grazing season. Nevertheless, set-stocked pastures in the first half of the grazing season are either understocked to allow a safety margin for the dry spell, with the result that the bulk of the herbage produced at the peak growth period is wasted; or they are too heavily stocked and supplementary feed is offered when the growth rate of the herbage fails to keep up with the animals' requirements. In both these ways, productive potential is wasted.

Rotational or 'paddock' grazing. It is generally accepted that the greatest production of herbage is obtained when grass is rested for a period, then defoliated rapidly and rested again, although this has not been fully investigated in grazing conditions. Evidence has already been quoted to show that with increasing frequency of defoliation the amount of herbage produced declines, but that the feeding value per unit weight increases (p. 35). The art of rotational grazing management lies firstly in finding the correct balance between the need for a high output per acre of herbage (which is encouraged by defoliation at infrequent intervals) and the need for herbage of sufficiently high quality for the animal in question; and secondly in devising methods *whereby a suitable sequence of rest and defoliation can be provided.* In current British practice, paddock size and stocking intensity are preferably arranged so that each paddock is grazed down in 4–7 days. To achieve this the stocking intensity should be about 10 cow equivalents per acre. The acreage available must, therefore, be divided into a number of fields or paddocks to permit a succession of grazing. A simple system involves the use of four paddocks—each one grazed for one week and rested for three weeks. But to permit the farmer to cope with the variations in rate of growth which occur it is preferable to have a larger number of paddocks, some of which should be cut for conservation when growth has been rapid. Such a system has been described in detail by Voisin (1951, 1959).

Although the advantages to herbage production of allowing long periods of rest have been demonstrated when the herbage was cut, comparisons of continuous and rotational grazing methods have not

always shown any marked advantage for the latter in terms of utilized output. The increase in production per acre has ranged from, for example nil (Carrier and Oakley, 1914, Holdaway and Pratt, 1933) to 9 per cent (Hodgson, Grunder, Knott and Ellington, 1933), from 12 to 15 per cent (New Zealand Department of Agriculture, 1954, 1955), and to 20 per cent (Woodward, Shepherd and Graves, 1933; Pratt and Davis 1954). When daily fold-grazing was superimposed on the rotational system (a procedure which might be expected to enhance any superiority of rotational grazing) the increase in utilized output compared with continuous grazing has varied from nil, when stocking rates per acre were equal but adjusted according to normal variation in herbage growth (Arnold and Holmes 1958) to 10 per cent, when stocking rates were similarly adjusted but not quite equal (Campling MacLusky and Holmes 1958) and 300 per cent, when stocking rates were adjusted in fold-grazing but not in continuous grazing (Brundage and Petersen, 1952).

Most of these experiments were carried out using dairy cows and it has been argued that the system is unsuitable for beef cattle and that these require undisturbed continuous grazing to minimize variations in the quality of the herbage consumed. It has not been clearly shown that beef animals are any more sensitive to variations in the quality of the herbage consumed than are dairy cows and the opposite seems more probable. Rotational grazing has however, sometimes given a slight reduction in output of beef per acre (Salter, Gerlaugh and Welton 1930, Comfort and Brown, 1933).

With sheep the difference between rotational grazing and continuous grazing has generally been small although Comforth (1955) found an increase in production per acre from rotational grazing when this was compared with continuous grazing. Lambourne (1956) in New Zealand showed that rotational grazing with ewes and lambs was superior to set-stocking at high rates of stocking per acre, but inferior at low stocking. (In set-stocking there is no variation in the stocking rate during the season.) Rotational grazing made more herbage available but whether the value of the system was realized depended on conservation. If part of the pasture was conserved and heavy stocking adopted on the remainder, the quality of the grazed herbage was improved and consequently the growth rate of the lambs. Without conservation the surplus herbage caused a deterioration in the quality of the pasture and a reduction in the lambs' growth rates.

That rotational grazing does not always lead to increased output

despite the advantages of rest periods shown in machine-cutting experiments is possibly to some extent due to a difference between cutting and grazing conditions (such as the longer duration of each period of defoliation in grazing as compared with cutting) but, as Table 2.7 shows, it is mainly due to poor utilization in the sense of wastage either in the field or in the animal (Bosch, 1956). Failure to adjust

TABLE 2.7. *The difference between herbage dry-matter production and utilized production at different frequencies of grazing* (Bosch, 1956)

100 lb. per acre approx.

No. of grazings in the year	Herbage dry matter		Herbage starch equiv.	Utilized starch equiv.	Loss in S.E. in utilization %
	per grazing	per year			
6	16	97	58	41	28
5	21	104	61	40	35
4	27	108	65	32	50

the stocking rate to the increased amount of herbage available, if the herbage is of good quality, may result in the animal consuming herbage in excess of its requirements or abilities for production: if the herbage is allowed to become too coarse when grazed there will be a decline both in intake and in feeding value and much of the herbage may be left uneaten (Waite, Holmes, Campbell and Fergusson, 1950; Van der Kley, 1956). In addition to possible wastage of surplus herbage, grazing stock are free to tread and to foul edible herbage before it is grazed. Although the amount of herbage so wasted is not usually very great, more damage is probably done this way than in continuous grazing, since in the rotational system a greater amount of edible herbage is concentrated on to a smaller area at each grazing. This, among the sources of wastage, increases with increasing yields of herbage (Bosch, 1950, 1956). Another drawback to rotational grazing is that the nutrient intake of the animal, and, therefore, its productivity, are subject to great variation (Raymond, Minson and Harris, 1956; Van der Kley, 1956). This arises from the grazing habits and preference of grazing animals. On entering a fresh field, cattle first of all 'tip' the herbage, that is, they consume the topmost leaf. This is the most nourishing part, as Table 2.8 shows. It is also the most palatable. As a result their intake of nutrients on the first day or two of grazing is very high,

TABLE 2 8 *Analysis of the leaf tips selected by cattle compared with the rest of herbage* (Gardner *et al* 1929)

	Crude protein	Ash	Silica
	(% in dry matter)		
Tip of leaves	27 2	11 9	3 2
Remainder of herbage	19 5	20 6	12 2

and probably greater than their requirements This may, in fact, encourage bloat or the development of other disorders such as scour Later, cattle select and concentrate on those parts of the pasture which were found to be most palatable when 'tipped , so that finally, in the last days of the grazing period the remaining herbage is of low quality and low palatability with the results that the intake of nutrients is extremely low and production suffers In practice dairy cows are normally removed before the available herbage is entirely consumed, so as to avoid a sharp drop in yields This has been deliberately done in New Zealand in a lax rotational grazing system which it has been claimed, leads to improved regrowth of the herbage (Stewart and Hyde 1954) This may be so on a uniformly dense and leafy sward but on a more typically uneven sward attempting to run to seed it is probable that if the residue is not removed there will be wastage of herbage and a deterioration in quality

Some of these difficulties can be overcome by allowing the stock with the highest nutrient requirements first access to the pasture and by following them with stock of lower requirements For example young calves may precede the milking cows and these may be followed by dry stock or beef cattle with ewes and lambs store cattle and store sheep may be grazed in sequence This procedure is often cumbersome in practice and depends on a convenient field layout It also reduces the period available for regrowth of the herbage and increases the risk of transmission of parasitic worm infections to succeeding groups of livestock of the same species Rotational grazing otherwise reduces this risk and it has been found particularly valuable with sheep in controlling worm infestations and also foot rot (Beveridge 1955)

Recently 'forward creep-grazing', a specialized form of rotational grazing has been introduced for fat lamb production on grass Ewes and lambs are heavily stocked in small paddocks but the lambs are

allowed access through the fence to the next paddock ahead in the rotation. Lambs therefore are able to consume the leafy material (which is not so heavily contaminated with worm larvae), while the ewes whose nutrient requirements are lower, follow the lambs and consume the basal herbage. Because of their superior resistance to worm infestation the ewes act as disinfectors of the sward. This and 'sideways creep-grazing', both of which have given very high outputs per acre, are further discussed in Chapter 11.

Close-folding: strip- or fold-grazing. The advantage to herbage growth of adequate rest periods can be gained, and the disadvantages of the rotational grazing system largely eliminated, by the use of an electric fence to supply grazing cattle with their herbage requirements day by day. This system has been variously called fold-, strip- or break-grazing, close-folding, and daily rotational grazing. It is generally desirable that a second fence (back fence) should follow behind the grazing stock (see Fig. 2.3).

Increases in output per acre from fold-grazing compared with rotational grazing may be found in practice for several of the following reasons: (1) selection by the grazing animal is limited so that there is less wastage and less variation from day to day in the quality and amount of herbage consumed; (2) depending on the stocking rate there may also be a slight reduction in the average amount of herbage consumed daily by each animal although its production is unaffected; (3) the chance of herbage being trampled and fouled before grazing is reduced; (4) the period for regrowth between each grazing is increased by several days, perhaps by a week or more, compared with rotational grazing. It is possible also that in certain conditions the close defoliation achieved by this system results in an increase in the rate of regrowth (see page 36). This will not hold true if the animals are allowed prolonged access to the grazed sward, for if the regrowth is grazed at this early stage the sward is deprived both of photosynthetic material and of its nutrient reserves and its vigour will be impaired. Finally (5) the fold-grazing system enables the amount of future grazing to be accurately assessed and makes it extremely easy to decide how much can be cut for conservation. This in practice is possibly the main virtue of the system.

Several workers using dairy cows have shown that compared with rotational grazing in paddocks grazed for 4–7 days, fold-grazing increased the utilized output of the pasture by from 16 to 45 per cent (de Geus, 1947; Holmes *et al.*, 1950; Procter and Hood 1953). Some

results of a comparison made at the Hannah Institute (Holmes *et al.*, 1950) are shown in Table 2.9 Although the folding system ignores

TABLE 2.9. *A comparison of the relative outputs per acre gained from rotation grazing and close-folding*

Production	Close-folding	Rotation grazing
Cow-days per acre	208	159
Milk yield per acre (gal.)	566	398
Live-weight gain per acre (lb.)	199	200
Utilized S.E. per acre (cwt.)	30	23

many traditional tenets of beef graziers, Hughes and Redford (1952) have reported trials with beef cattle which showed superior results for the fold-grazing system. This has been confirmed by Ittner, Lofgreen and Meyer (1954) in the United States, who found an increase of 36 per cent in the output of beef per acre from fold-grazing as compared with rotation grazing.

In most of these experiments stocking rates per acre were not kept equal on the two grazing systems. It has been suggested by McMeekan and Hancock (1954), however, that similar yields per acre and per animal can be obtained in rotation grazing if the animals are beld on the pasture and forced to eat the herbage as closely as they do in fold-grazing, that is if stocking rates are kept exactly the same. It is now clear that in experimental conditions this can be done (Brundage, Sweetman, Hodgson and Bula, 1956; Brundage and Sweetman, 1959; Freer, 1958), but the difficulty in practice with rotational grazing is to decide when to move the cattle to a fresh pasture without either wasting berbage by moving the cattle too soon, or depressing their production by leaving them too long.

In a comparison between fold-grazing and rotation-grazing, conducted at the Hannah Institute in 1956 on a perennial ryegrass sward, the assumption was made that if stocking rates were equal no difference was to be expected between the two systems and that if, therefore, five paddocks were each divided into two, and one half fold-grazed (with electric fences both before and behind the cows) and the other rotation-grazed by similar groups of cows on exactly the same days throughout the season, no difference in herbage yields or milk production could result. It was found that there was a 28 per cent superiority in herb-

age yield in the fold-grazed paddocks at the start of each grazing period. The use of the 'back-fence' was probably important in achieving this result. The cow groups were changed from one system to the other every 4 weeks for 4 months, and the resulting milk yields were as shown in Fig. 2.2. Although (as in a very similar experiment of Brundage and Sweetman, 1959) there was no difference in mean yield per cow or in utilized output between the two systems, within each period of this experiment there was a tendency for milk yields to decline faster in rotation-grazing than in fold-grazing. This might have entailed a substantial difference in yield in the long term had each lot of cows remained in one system continuously. This effect may have been due either to the variability of milk yields in rotation grazing, or to the superiority in the yield of herbage dry matter with close-folding in this particular year, or possibly to both causes. Despite the similarity of the mean milk yields, consideration of the superiority of herbage yields in fold-grazing, and the greater tendency for milk yields and the rate of live-weight increase to decline in rotation-grazing, suggests that had the stocking rates in each system been separately adjusted according to the amount of herbage available, there would have been an increase in stocking rates in close-folding or a reduction in rotation-grazing with a consequent difference in utilized output per acre.

In a recent experiment which compared fold-grazing with continuous-grazing (where substantial differences in herbage yields might have been expected), and in which stocking rates were adjusted according to seasonal variation in herbage growth, but kept the same in each system, no difference in utilized output per acre was found. It is possible, however, that differences in herbage dry-matter yields and consumption existed which failed to influence the productivity of the cattle (Arnold and Holmes, 1958). It has already been suggested that outside experimental conditions such careful adjustments of stocking rate or acreage according to seasonal variations in herbage growth are not so easy either in continuous or rotational grazing methods as they are with fold-grazing.

Whether or not fold-grazing gives an increase in output depends largely on whether the virtues of the system as a means of increasing and adjusting the intensity of stocking per acre are realized. At low intensities there is no advantage since the animals are not then obliged to graze the herbage closely to the ground, but simply 'skim the cream off' the pasture each day, and graze selectively. At very high

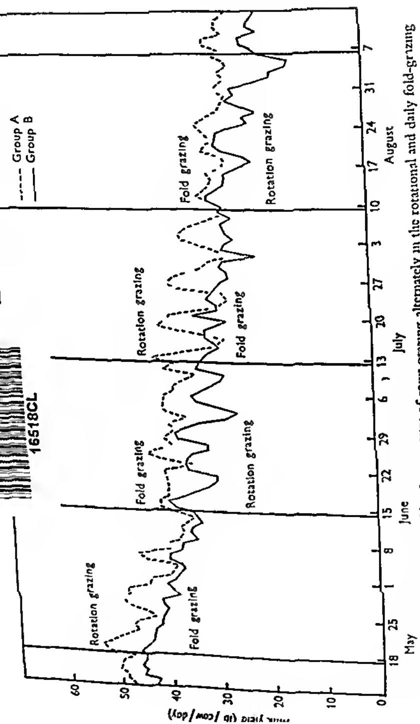

FIG 2 2 The mean daily milk yields of two groups of cows grazing alternately in the rotational and daily fold-grazing systems during 4 periods each of 4 weeks

16

intensities of stocking there is insufficient freedom of movement, grazing behaviour is disturbed, grazing is uneven and the amount of herbage made available may be inadequate for the animal's requirements. Depending on the yield of herbage, the stocking intensity should be between 40 and 80 cows to the acre, or the equivalent. In practice, the stockman quickly learns to judge the optimal stocking intensity on a given sward.

Because selection in grazing is almost eliminated by fold-grazing, the animal is more dependent for its needs on the farmer's ability to provide good-quality herbage than it is in any other grazing system. This method, in fact, can only be used with success on good-quality herbage. The effectiveness of fold-grazing is probably also related to the type of sward on which it is practised. With a close-knit ryegrass sward the variation in feed composition from day to day under rotational grazing is likely to be much less than on an open sward of erect grasses such as cocksfoot or lucerne. Any benefit from daily fold-grazing in maintaining uniform feed intake is, therefore, likely to be greater in the latter swards. In some areas it has been found useful chiefly in the spring and early summer because the pasture is fouled by dung after two or three grazings, but in other areas it has been used throughout the season with success. Frequent rainfall is probably essential for the disposal of dung. However, in all circumstances the fouling effect of dung (MacLusky, 1960) is greatly reduced if after the second or third grazing the herbage is allowed to grow and then cut for silage, after which the regrowth is again clean and palatable.

There are several ways in which the high stocking intensities necessary for successful close-folding may be achieved (Fig. 2.3). The best utilization of the herbage, involving the cleanest and least selective grazing with the least fouling and treading, results when the day's allocation of herbage is offered to the herd on a long narrow strip. The term 'strip-grazing' is perhaps best used to describe this particular system and the term 'fold-grazing' used when the area grazed daily approaches a square shape. Provided the herd is allowed space for movement on herbage already grazed, strip-grazing ensures that most of the fresh herbage is consumed and not fouled, since much of it will, in fact, be beneath or beyond the electric fence, and cattle must reach for it. The herbage beneath and beyond the fence is usually grazed most closely and with the least selection.

Alternatively, the field can be divided in any other of the ways shown in Fig. 2.3. In practice, it is often convenient to divide big fields into

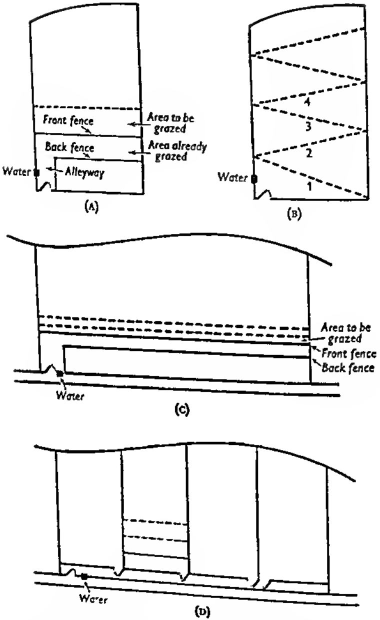

FIG 2 3 Various methods of close-folding and strip-grazing
(A) Parallel fencing showing front fence back fence and alleyway to gate and water
(B) Span or diagonal fencing showing successive positions of electric fence
(C) Strip grazing the disadvantage is the length of the fence for moving
(D) Alternative to (C) the field is divided into small paddocks which, depending on their size may be fold-grazed.

smaller paddocks with semi-permanent fencing, each paddock of a size to carry the herd for 4–7 days and then to fold the cattle daily within each paddock. This reduces the length of the grazing front, and the length of the alleyway, and, although it involves greater initial expense, it reduces the amount of time spent on fence-moving each day. Provided the paddocks are not too small, this system also allows greater flexibility in utilization. If the size of the paddocks is such that each allows only a day's grazing for the herd (as in New Zealand 'paddock-grazing'), the system becomes very little different from fold-grazing (except that in 'paddock-grazing' in New Zealand severe defoliation is avoided). With larger paddocks a back-fence should be erected 1–2 days behind the cows to keep the animals from consuming the early regrowth of the grazed herbage.

Some graziers have extended the folding principle further and move the cattle to a fresh fold twice daily. Although in principle this should ensure very efficient grazing it doubles the labour cost and Flux and Patchell (1955) detected no advantage in yield per cow or per acre.

Restriction of grazing time. Instead of restricting the area available to cows, attempts have been made to restrict the time allowed for grazing by the cow, for example to three grazing periods daily, each of one hour or less. These attempts ignore the results of behaviour studies which show that dairy cows normally spend certainly no less than 7 hours in active grazing even on high-quality herbage (e.g. Waite, MacDonald and Holmes, 1951; Hancock, 1953). The cow's rate of herbage intake increases when the grazing time is limited (McCullough 1959), but the threefold increase which would be necessary to ensure adequate fill in 2–3 hours of grazing is hardly to be expected. Other examples may be cited which suggest that grazing management must take cognizance of the cow's normal habits. Wussow, Hartwig and Dietrich (1954) and Vik (1956) found that limiting dairy cows to grazing only during the day period, or during the night period (i.e. p.m. to a.m. milking) reduced their production of milk and milk fat compared with their production when they were allowed grazing at any time in the 24-hour period. Only in hot climates such as those of the southern United States could the restriction of grazing to the night period be expected to show an advantage (Hancock, 1953).

Soilage, 'zero-pasture' or mechanical grazing. The most complete utilization of pasture herbage results when the herbage is cut and carted to the stock. This sytem is traditional in some parts of Europe where

pastures are inaccessible to stock or where the utmost efficiency of utilization is required because of short growing seasons, or poor growth, and where until recently labour has been more easily provided than land. But it is at present attracting increasing attention in the United States where mechanization may make it cheaper to take grass to the cows than to take the cows to grass. The 'zero-pasture' system, as it is called in the United States, results in very efficient utilization (for example, Hoglund, 1956). But the type of pasture used is often of the sort in which poor utilization by grazing cattle might be expected, e.g. Sudan grass (*Sorghum sudanense*) which is long, fibrous and subject to wastage by treading and fouling. The advantages of the system are, therefore, more pronounced on such pasture types than on short leafy pastures.

A drawback to the system is that selection is completely eliminated. Even on fold-grazing excessively fibrous basal herbage is refused by the cows, and if this occurs the stocking intensity can be reduced and the stubble mown. But when pasture is mown all the herbage grown, including fibrous material, is offered. Consequently feed intake and animal production may suffer. The animal's preferences are, in this particular context, a useful guide to the feeding value of the herbage and the soilage system ignores them. It was probably for this reason that in a recent comparison at the Hannah Institute between soilage, fold-grazing and fold-grazing on cut and wilted herbage, on a rye-grass–clover sward, a depression of live weight and milk yield was found with cows on the soilage system (Table 2.10). It may be that with

TABLE 2.10 *The effect of different systems of offering herbage to dairy cows on their milk yields and live weight*

Production	Strip grazing	Strip grazing plus supplementary feed	Strip grazing on herbage which has been cut	Housed cattle fed on cut herbage
Milk yield (lb per cow per day)	31	32	29	28
Live weight per cow as % of strip grazing	100	101	101	97

very young succulent herbage such as that produced by frequent gang-mowing, better animal production would have resulted. Trials by

Runcie (1959) at Edinburgh have shown slightly lower outputs both per animal and per acre from the soilage system when compared with fold-grazing.

FACTORS AFFECTING THE AMOUNT OF HERBAGE CONSUMED BY THE ANIMAL

Although in general the amount of herbage consumed daily is related to the live weight of the animal, there are deviations from this rule which result from variations in the quality of the herbage, from differences in appetite between animals, and from the grazing system.

Allowed free choice, cattle and sheep normally select herbage of the highest digestibility and crude protein content and lowest fibre content: that is, young and succulent leaf rather than coarse leaf or stem. This is true for selection in pastures containing various qualities or species of herbage and probably also explains the preferences cattle show among different herbage associations on hill grazings (Archibald, Bennett and Ritchie, 1943; Hardison, Reid, Martin and Woolfolk, 1954; Pearsall, 1950). The reason for this preference is probably that the least fibrous herbage is the easiest to consume. The amount consumed daily increases with the digestibility of the herbage, not only because it is more palatable, but also probably because it occupies less space in the alimentary tract and requires less time for rumination (McCullough, Sell and Neville, 1954). The ruminant, of course, requires some fibrous food and on herbage which is very leafy and low in fibre it will consume some straw or coarse hedgerow material.

The amount of herbage consumed daily by bullocks and by dairy cows decreases with decreasing yields of herbage per acre. Johnstone-Wallace and Kennedy (1944) showed that as grazing continued and the yield of herbage declined bullocks consumed less and less herbage daily. This was because the proportion of palatable leafy herbage declined and the remaining herbage became shorter, more fibrous and so more difficult to graze. In experiments with cattle grazed in paddocks which supplied only one day's grazing, the daily herbage consumption increased both with increases in yield of herbage at a given rate of stocking per acre, and with reductions in the rate of stocking per acre at a given yield of herbage. In both circumstances, the quantity of herbage available to the cows was increased, there was more opportunity for the animal to select and less need for the cows to graze the coarser basal herbage (MacLusky, 1955). Of course,

when a very high herbage yield is reached due to increasing maturity, the rate of consumption declines (Waite *et al*, 1950) Mature herbage is less palatable and less digestible, and its rate of passage may be delayed by the need for prolonged rumination

The feed consumption of cattle is also probably affected by the level of milk yield although cause and effect are rather difficult to segregate in this connection However, Sjollema (1950) quoted variations in appetite with milk yield, which experiments by MacLusky (1955) with grazing cows tend to confirm Dry cows consumed amounts of dry matter equivalent to about 2 0 per cent of their live weight daily, while cows yielding 40 lb milk per day consumed the equivalent of 2 7 per cent of their live weight (see also Jarl, 1952, Kruger and Muller, 1955, McCullough, 1959) Cox *et al* (1956) and Wallace (1956) have related the herbage intake of milking cows to live weight, rate of live weight gain and milk yield

These observations help in comparing the effects of different grazing systems on the animal In continuous grazing at heavy stocking intensities, cattle probably consume moderate amounts of high-quality herbage daily and most of the herbage produced is utilized At low stocking rates cattle are allowed to select and probably consume greater amounts of high-quality herbage If the stocking rates are extremely low the herbage may become entirely coarse and the amount and quality of the herbage consumed may then decline Unfortunately few estimates of the amounts consumed by cattle in continuous grazing are yet available, but in one recent estimate cows in a continuous-grazing system at a fairly high stocking rate per acre were found to consume amounts of digestible organic matter daily which in terms of dry matter were equivalent to about 2 7 per cent of their live weight (Arnold and Holmes, 1958)

In rotational grazing the quality and amount of herbage consumed depend on the stage of growth of the herbage when the cattle are turned in, and on the intensity and duration of stocking At low intensities and short durations of stocking, cattle can select high-quality herbage and are not subject to the difficulties of grazing the short and fibrous basal herbage In optimal conditions, dairy cows yielding 30 lb of milk daily may be expected to consume daily amounts of herbage dry matter equivalent to 2 8 per cent of their live weight (Waite *et al*, 1950) In similar conditions beef cattle have been estimated to consume herbage dry matter equivalent to about 2 4 per cent of their live weight daily (Linehan, Lowe and Stewart, 1952)

In fold-grazing, little selection is possible and close grazing is, or should be, obligatory. The dry-matter intake of dairy cattle does not then reach the level found in rotational grazing, but averages about 2·4 per cent of the live weight (Waite *et al.*, 1950; MacLusky, 1955; Cox *et al.*, 1956). Variations may be expected according to the quality of the herbage offered and the closeness of grazing enforced.

RELATIVE PRODUCTION PER ANIMAL AND PER ACRE

From what has been said it is obvious that the grazing conditions which encourage the highest daily rate of herbage consumption per animal are not always those that lead to the greatest utilized output of pastures. High productivity per animal is of little value to the farmer without high output per acre, and a balance must be struck between the two.

The highest yields of herbage per acre are probably obtained by infrequent defoliations, but the utilized output increases only within limits because at the highest yields the herbage becomes less palatable and of lower feeding value, and even when fold-grazing is adopted wastage from treading and fouling increase. For this reason Bosch (1950, 1956) found that as the length of the herbage grazed increased, the yields of utilized dry matter and starch equivalent declined, although the total yield of berbage increased.

With dairy cows on intensively fertilized and rotationally managed pastures, the balance between quality and yield appears to be obtained when the berbage is grazed at the long leafy stage, that is, at intervals of about four weeks, and the maximum output of milk per acre is ensured by fold-grazing. Although in this system neither the quality nor the amount of herbage consumed is as high as it would be, for example, in lenient rotational grazing on younger herbage, there is a negligible decline in production per cow, and an increase in output per acre. There is, in fact, little decline in the feeding value of herbage to the long leafy stage, and the reduction in the amount of herbage consumed is presumably compensated by an increase in the efficiency of food utilization by the animal (Blaxter and Graham, 1955).

It might be argued that if cows were allowed to do so, they would select the most nutritious herbage and so yield more milk, but any such increase in yield would be very slight, and because it would entail wasteful utilization, the output per acre would decline. In a recent experiment at the Hannah Institute (Campling *et al.*, 1958), some selection was permitted by allowing cows continuous grazing on a clover

sward, and the milk production per cow and per acre from this system were compared with the production obtained on continuously-grazed swards treated with compound fertilizer, and with that obtained using the same amounts of fertilizer on a fold-grazed sward. It was found that there was no difference between systems in yield per cow, although, of course, there were very marked increases in milk yield per acre with the intensive fertilizer treatments. The output per acre from the continuously grazed swards was as much as 90 per cent of that from the fold-grazed swards, as a result of making careful variations in the stocking rate on the continuously-grazed swards to correspond with seasonal variations in the rate of herbage growth (Campling, MacLusky and Holmes, 1958). For the same reason, in a similar experiment at Wye College in Kent no difference was found between these grazing methods (Arnold and Holmes, 1958). In an American experiment comparing continuous- and fold-grazing methods in which the stocking rate of a fixed number of fold-grazed cows was increased when herbage growth was vigorous (the surplus herbage being conserved) but in which no adjustment was made with the continuously-grazed cows, the free selection permitted to the continuously-grazed cows by their relatively low stocking rate gave no increase in production per animal, and a low utilized output per acre (Brundage and Petersen 1952). Stocking rates can on the other hand be increased to the extent that intake per animal is limited and even reduced without loss in production per animal (Waite, Holmes, Campbell and Fergusson, 1950, Ivins, Dilnot and Davison, 1958) and in reviewing New Zealand experiments in which outputs per animal and per acre under different stocking rates and grazing methods were investigated, McMeekan (1956) has suggested that output per acre is governed primarily by stocking rate. In considering relative outputs per animal and per acre in grassland evaluation Ivins *et al* (1958) have drawn attention to the need to consider the potential productivity of both the grass and the stock, either of which may at different times act as a limiting factor to utilized output per acre.

THE EFFECT OF SUPPLEMENTARY FEED ON PRODUCTION PER ANIMAL

The effect of supplementary feed on the amount of herbage cattle consume daily depends on the relative palatability of the herbage and the supplement, and this is generally related to their digestibilities or theoretical starch equivalents. Grain or cattle cake offered in amounts

up to 8 lb. daily only slightly depresses consumption of good-quality herbage, but probably depresses to a greater extent the consumption of fibrous and unpalatable herbage. Dry roughage supplements are unlikely to be consumed in any quantity unless the pasture is of very poor quality or extremely lush and immature, or when the animal's hunger is otherwise unsatisfied. Increases in animal production from supplementary feeds are seldom economic. In experiments at the Hannah Institute dairy cows yielding up to 35 lb. daily and receiving up to 8 lb. oats or dairy cake produced an increase of only 0·3 lb. milk per lb. supplementary feed (MacLusky, 1955). Similarly uneconomic increases have been found at the Rowett Institute (Corbett, 1958). In a series of Danish experiments, the increase in milk yield obtained per lb. of concentrate supplement fed ranged from 0·5 to 1·4 lb., and in two series of Dutch experiments, increases of 0·25 and 0·35 lb. of milk per lb. supplement were obtained (Steensberg, Eskedal and Ostergaard, 1931; t'Hart, 1956). The relative costs of feeding stuffs and milk generally make such increases uneconomic except when the amount of grass available is limited because of drought or some other reason. Even in such conditions the provision of good-quality roughage feeds, such as silage, is cheaper and as effective.

Sjollema (1950) claimed that high-protein pastures (over 20 per cent D.C.P.) were harmful to the health and milk yield of cows in mid-lactation and recommended restriction of pasture intake and supplementation with starchy food. At lower protein contents in pastures, which are more common, no beneficial effects from supplementary feed of high starch content have been detected in trials at the Hannah Institute, although low-protein concentrates increased the rate of live-weight gain more than did high-protein concentrates. Maize, a low-protein high-energy concentrate, has been found in certain conditions to increase the solids-not-fat content of milk (Corbett, 1958).

Observations with beef cattle have failed to reveal economically significant increases in live-weight gain from supplementary feeding provided good pasture was available (Alder, Head and Berting, 1956).

THE MECHANICAL TREATMENT OF PASTURES

Harrowing. Grassland may be harrowed in the spring to tear out dead herbage and to aerate the sward and may be harrowed later in the season to spread dung. It is doubtful, however, whether harrowing during the growing season is worth while. On land grazed by cattle, harrowing smears soft faeces over even larger areas of grass which

remain fouled until rain falls If the dung is already dried hard, harrowing may have little effect in spreading it Sheep dung is more readily spread by harrowing, but since it falls in smaller lumps than cow dung, it is less objectionable on a pasture Recently it has been suggested that harrowing may spread parasitic worm larvae (Hignett, 1956), and since this provides aerobic conditions it may, unless the larvae are dessicated, facilitate their survival (see Chapter 18) For various reasons, therefore, harrowing has little to recommend it during the grazing season

Trimming The mowing machine is essential for the proper control of grassland. In most circumstances, the use of the mowing machine at least once in the growing season is needed, both to remove coarse unpalatable herbage and to encourage the production of leafy tillers by suppressing the growth of flowering stems Moreover, this practice controls many grassland weeds (e g thistles, buttercup and ragweed)

Sometimes reference is made to the practice as 'topping' but to encourage the production of leafy tillers the herbage should be cut not at a height of 3–5 in from ground level, but at 1–2 in from ground level. The herbage which is cut should, of course, be utilized It is usually most convenient to let grazing stock eat it off, preferably those which do not require very high-quality feed

Gang mowing The use of gang mowers (teams of rotary cylinder mowers) has been found to be very successful in maintaining the high quality of ryegrass pastures continuously grazed by sheep in south-east England This treatment is not applied to trim coarse overgrown herbage nor to mow long herbage, but is used to prevent short, leafy herbage from becoming long (Chippendale and Merricks, 1956) Gang mowing would presumably not give such successful results with species or strains of grass other than those able to withstand continuous grazing or close-cutting, in particular perennial ryegrass Experimental studies suggest that the value of gang mowing lies both in the encouragement of leafy growth and in the invigoration of clover (Cornforth, 1955) In conjunction with a forage-loader and trailer the gang mower can be used to provide very high-quality herbage for ensilage (Hunt and Montgomerie, 1958) The use of the gang mower is limited on stony land or with coarse herbage, but other types of mower such as the Hayter (horizontal revolving discs edged with small blades) can be used to equally good effect for the control of pasture quality in these conditions

CONSERVATION AND GRASSLAND MANAGEMENT

Some aspects of the techniques of different methods of conservation will be discussed briefly in the next sections of this chapter. Here conservation methods will be considered as an integral and important part of pasture management. In the past certain fields, often permanent meadows, have been set aside for hay, the only means of conservation, and any pasture herbage surplus to the needs of the grazing stock has generally been wasted. Perhaps the main feature of modern grassland management by contrast is the increased flexibility in utilization that is now possible (dependent in the first place on controlled grazing methods) which means that the herbage surplus to the needs of the grazing animal can now be conserved by the methods best suited to the management of herbage available. In this way conservation and grazing are integrated to the mutual benefit of summer and winter feeding.

Haymaking is of limited value as an aid to pasture management for it is very much dependent on dry weather and in most seasons is limited in use to a short period in early summer, when it creates a peak in labour requirements. To ensure quick drying, herbage intended for hay is usually cut at an advanced stage of growth, which not only entails poor feeding value (regardless of losses in the drying process) but results in delayed recovery of the sward and a deterioration in the denseness and palatability of the sward for grazing purposes. The effect of haying on the botanical composition of the sward may be critical and careful management is required to remedy its effects.

Artificial dryers can play a very useful part in grassland management in that any surplus herbage can be conserved at an early stage of growth without loss in feeding value, but dryers have not become popular because of the relatively high cost of the product. The best means of conservation for integration into a scheme of pasture management is ensilage, for grass silage is less dependent than hay on prolonged dry weather, and can be made at almost any time in the grazing season; as a result the work involved can be spread over the season more easily than with hay. The quality of herbage which can be ensiled is higher than that cut for hay, and unlike artificial drying the process is cheap, and does not necessarily entail heavy initial capital expenditure. Finally silage cuts can be taken with less drastic effects on the composition, texture and rate of recovery of the sward than those of haymaking. This allows some alternation of grazing with silage cuts, which reduces

wastage resulting from the effects of animal excrements on the palatability of the sward. A drawback to the use of silage as a tool in grassland management is that good silage cannot normally be made from successive small additions of herbage to the silo a fairly large quantity of herbage is necessary at any one filling to ensure a proper control of fermentation and uniformly good quality in the product Ensilage does not therefore eliminate the need for careful planning in grass utilization An exception to this is possible with the use of the gang mower and appropriate loading equipment (e g the Walley 'Gangmo-loader') over the whole of the farm pastures at frequent intervals to remove uniformly short, leafy and highly digestible herbage which requires little or no consolidation and which can be ensiled in successive small additions to the length of a pit silo (Hunt and Montgomerie, 1958, Turner, 1958) Silage need not be made to the exclusion of hay, but may indeed result in an improvement in the quality of hay by reducing the amount of grass which need be cut in the limited haymaking season, thus permitting more efficient haymaking techniques to be adopted.

METHODS OF CONSERVATION

It is not appropriate to discuss in detail here the problems and techniques of each conservation process, and only an outline of some of their main features will be given. For a fuller account of the intensive studies of conservation processes that have been made, the reader is referred to Watson (1948, 1951), Dijkstra (1954, 1959) and to Chapter 6, and for a detailed account to Watson and Nash (1960) Approximate relative feeding values and costs of dried grass, silage and hay are shown in Table 2 11

TABLE 2.11 *Approximate starch equivalent (S E) contents and costs for crops and concentrates in 1957*

	S E in the dry matter	Cost of S E. (£ per ton)
Grazing	55–75	12
'Early bite'	65–75	15
Grass silage	35–60	23
Hay	25–40	22
Dried grass	35–65	40
Dairy cake	70–80	46

Hay. Traditionally hay has been the only form in which grass has been conserved. It continues to be the cheapest and most widespread method of grass conservation, but the product is usually of poor feeding value. Because herbage is more easily made into hay when fully mature, and because the yield per acre continues to increase until quite late in the growth cycle, most hay is cut when too mature and fibrous with a low content of crude protein, carotene and minerals, and with a low starch equivalent. Losses in conservation reduce the feeding value even further.

Earlier cutting gives herbage of higher feeding value, but reduces yield per acre and increases the difficulties of drying. Higher yields of good-quality hay may be obtained by the application of artificial nitrogen early in the season and higher crude protein contents by nitrogen applied ten days before cutting (Moon, 1954). The liberal use of nitrogenous fertilizer for hay may, however, increase the difficulties of drying. The use of tripods and other devices facilitates the natural drying of immature herbage, but these, of course, limit mechanization and may increase the cost. Cheap hay, therefore, is unfortunately almost always a poor feed. Its starch equivalent is unlikely to exceed 40 and may be very much lower.

Baling in the field with the pick-up baler has become common in recent years. This reduces labour requirements and in the right conditions can reduce nutrient losses by reducing mechanical loss of leaf and by allowing the stacking of hay earlier than would otherwise be possible. In practice, however, baling leads to a reduction in quality if baling is done too early and the bale is made too dense relative to the moisture content of the grass. Early baling (and stacking) are easiest when the 'press' type of baler is used (rather than 'ram' or 'roll' types) since this makes loose, low-density bales which allow relatively easy air circulation even when stacked.

Another development which offers scope for improvement in quality is the use of a mechanical conditioner to bruise, or of a flail-type forage harvester to lacerate the grass immediately after mowing. This ensures quick drying even of immature herbage (given a short spell of dry weather) and the herbage can be baled and stacked very much earlier than would otherwise be possible. This technique increases the element of chance in haymaking when the weather is unsettled, for with heavy rain and delay in baling, nutrient losses will be increased instead of reduced.

Dried grass. The value of artificial drying is that it permits the

conservation of herbage at its youngest and, therefore, most nutritious stage of growth, and with the minimum loss of nutrients Moreover conservation may take place throughout the growing season Losses of starch equivalent in artificial drying rarely exceed 10 per cent The best-quality dried grass has about the same nutrient content as oat or barley grain, and can be used as a concentrate feed for dairy cows

In its early days artificial drying appeared to offer the best possible means of conservation, but there are three main objections to the practice for general use at the present time The first is the high capital outlay required The second is that the cost of drying has increased to the point at which dried grass costs as much as other feeds of equal feeding value, and the third is that the installation of a drier makes great demands on the organization of the grassland production, since, to justify the capital cost, a regular supply of herbage is required throughout the season The production from grass-clover swards, particularly ryegrass-clover swards, is generally too low and too variable for grass drying and special swards of grasses suitable for regular cutting must be grown The liberal use of artificial fertilizers is essential and in the drier areas of the country the extensive use of lucerne is necessary Thus a drier, instead of functioning as a useful tool in grassland management and conservation, becomes the arbiter of the grassland management programme.

Silage The process of ensilage has the virtue that herbage less mature than that suitable for hay can be conserved without such expensive capital equipment as that required for artificial drying Very young herbage is not usually ensiled because of its very high protein and low fermentable carbohydrate content which too easily result in undesirable types of fermentation and consequent high nutrient losses The quality of herbage ensiled is usually therefore midway between the qualities suitable for hay and for artificial drying Even with this sort of material, losses of 15–30 per cent of the dry matter ensiled may be expected (Watson and Smith 1951) and the greatest nutrient losses unfortunately are in the soluble carbohydrate fractions (Watson and Nash 1960) These losses are however, no greater than those involved in haymaking, and because the quality of herbage which can be ensiled is higher in the first place the nutritive value of silage is usually higher than that of hay and yet like haymaking the process is a cheap one Attempts to reduce the nutrient losses in fermentation especially of very leafy herbage, have included three sorts of additive mineral

acid, readily fermentable carbohydrate and chemical preservation agents of various sorts including sodium metabisulphite.

The addition of mineral acid (the A.I.V. process) has been claimed to ensure the right degree of acidification and to reduce losses in fermentation. Despite the better control of acidification that mineral acid allows, the process is losing favour in the countries where it has been developed and is rarely, if ever, used in this country. The acids are very dangerous to handle and the process requires constant responsible supervision. The silage also requires the addition of a neutralizing agent when it is fed to cattle.

The addition of a readily-fermentable carbohydrate such as molasses, or ground grain (Archibald *et al.*, 1954), encourages the development of a desirable lactic fermentation and has been shown to reduce the losses of dry matter and starch equivalent. Unlike mineral acid, molasses has the virtue of being innocuous and easy to apply. But in practice it is common to dispense even with the use of molasses, because in May and June the fermentable carbohydrate content of grass at the long leafy stage of growth is sufficiently high to encourage proper fermentation. Skill in adjusting the depth of herbage ensiled at any one time, and the amount of consolidation, according to the moisture content and density of the herbage, are then of vital importance since these control the amount of air present for respiration and the character of the subsequent fermentation. When pits or clamps are used consolidation by tractor presents no real problem, but because this silage-making system is easiest when fairly stemmy herbage is used, there is a common tendency to sacrifice the quality of the herbage ensiled for ease of making and for tonnage.

Sodium metabisulphite has recently been introduced as a preservative agent. Recent trials in America, New Zealand, and this country have shown variable and in general disappointing results. Some reduction in nutrient losses and improvement in digestibility have been found with immature herbage, but the improvements were too small to justify the cost (Smith, 1960). The only consistent advantage reported is the reduction it brings about in the smell of silage (Murdoch, Holdsworth and Wood, 1956; Smith, 1960). This is not unimportant, for the smell of silage has often been responsible for prejudice against its use.

Two factors which from recent work in this country appear to offer scope for improvement in the feeding value of silage at the present time are control of the maturity of the herbage ensiled and of the

dry-matter content of the silage Maturity not only directly affects digestibility and the dry-matter content of the silage but also affects the amount of silage dry matter consumed In practice this means that herbage should be cut before it has become unduly stemmy, and allowed to wilt for 24 hours before ensiling and the silage should be protected from rain by some effective cover While earlier cutting gives material of higher digestibility it also normally results in lower dry-matter content Attempts to raise dry-matter content, however, should not be made at the expense of digestibility, for the dry-matter content of silage declines in importance as the digestibility of the dry matter increases and wilting of immature and highly digestible material can effectively increase the dry-matter content

in some sections of the industry and on some farms. One farmer in every three of nearly a thousand recently surveyed by the Milk Marketing Board (1959) made silage, and on some farms silage provides virtually the entire winter feed requirements of the stock.

UTILIZATION OF CONSERVED GRASS FEEDS IN LIVESTOCK RATIONS

Although well-managed pastures can supply all the requirements even of high-yielding dairy cows, the same cannot be expected of conserved grass feeds, because grass is usually cut for conservation at a more advanced stage of growth, and therefore lower nutritive value, than pasture, and because further losses in nutritive value occur during conservation. Moreover, cattle show a lower appetite when fed grass feeds alone than when some concentrate feed is included in the diet (see, for example, Holmes *et al.*, 1957). While the contribution of grass to livestock feed requirements has been estimated to be 67 per cent in 1934–8 (Wright, 1940) and about 70 per cent in 1952–3 (O.E.E.C., 1954), in the Netherlands the contribution of grass has been estimated to be about 80 per cent and on some farms in this country grass feeds provide practically all the annual feed requirements of the stock. There is therefore scope for increased use of grass in livestock rations, but to this generalization must be added the proviso that consideration must be given to the choice of grass product and the particular requirements of the animal to which it is fed.

The nutritive value of hay does not normally justify its occupying a large proportion of rations for dairy or fattening cattle, and when it has done so in the past highly concentrated imported feeds have been fed along with it. When silage is used, hay is still useful as a means of giving some variety to the ration and it probably increases the animals' daily feed intake and production (Dijkstra, 1959).

Satisfactory gains in weight can be made when silage alone is fed to growing cattle and to sheep, and good-quality silage is adequate for fattening purposes (Dodsworth and Campbell, 1953). When dairy cattle are fed a diet composed entirely of silage, however, the quantity of nutrients consumed may be inadequate for high milk production and the solids-not-fat content of the milk may be lowered (e.g. Holmes *et al.*, 1956; N.A.A.S., 1954). Although profitable levels of milk yield have been reported from feeding silage alone, an improvement in both the yield and quality of the milk can generally be obtained economically by feeding some concentrates. Grass feeds because of

their high protein content relative to their energy value usually reduce the need for high-protein imported feeds, so that home-grown grains or other cheap concentrates of medium protein content are adequate except for the highest yielding cows But the optimal economic level of concentrate usage when good-quality grass feeds are available is a matter of some controversy in dairy farming which is referred to briefly again below

THE ECONOMICS OF GRASS PRODUCTION

This discussion of grassland management would be incomplete without reference to its economic aspects, although since these are complex and somewhat controversial it is impossible to deal with them fully here It is well established that, compared with most other feeding stuffs, grazing in particular and grass products in general are extremely cheap (Hamilton, 1956, Committee on Grassland Utilization, 1958) The important economic questions are: first, to what extent grassland production can be profitably increased, and second, how the extra production should be utilized—whether it should be used to increase turnover by increasing the stock-carrying capacity of the farm, or whether it should be used to reduce the costs of feeding by increasing the proportion of grass in livestock rations In practice there is no sharp distinction between these approaches, but it is convenient to take the two extreme policies as a basis for brief discussion

INCREASING GRASS PRODUCTION

Many factors involved in increasing grass production are difficult to assess either quantitatively or in terms of cost, and it is common to regard fertilizer usage, especially of nitrogenous fertilizer, as the most important factor But it must be stressed that improvements in grassland management in various ways may result in considerable increases in production and profitability with little expenditure on fertilizer (see, for example, Heady and Jensen, 1954) It has been recently pointed out that improvements in grass production and utilization depend in the first place on increases in the efficiency of the management of the farm as a whole (Committee on Grassland Utilization, 1958)

So far as fertilizers are concerned, however, provided the grass produced is effectively utilized the extra cost is justified in principle so

long as the value of the extra herbage produced is greater than the cost of the fertilizer and its application. Table 2.12 shows some examples

TABLE 2.12. *The cost of producing additional grass with fertilizer*

Net response per 1 lb. nitrogen (lb. dry matter)	Cost of fertilizer per ton additional grass dry matter (£)	Cost of fertilizer per ton of additional S.E. (£)
5	25·0	45·5
10	12·5	22·7
15	8·4	15·2
20	6·3	11·4
25	5·0	9·1

It is assumed that N, P_2O_5 and K_2O are applied in the ratio *3:1:3*.
Fertilizer prices are those current in Britain in *1956*.

of the cost per ton of additional dry matter, of the application of a complete compound fertilizer over the range of response likely to be encountered. Within the most common range of responses found with herbage at the leafy to long leafy stage of growth (10–20 lb. dry matter/lb. N), this shows that the cost of the extra herbage is little greater than that of pasture receiving no fertilizer. Allowing for the costs of conservation the extra herbage at this level of response is produced at a cost which compares favourably with alternative feeds (see Chapter 4). The point at which the cost exceeds the value of the herbage produced is only found at the lower levels of response shown in Table 2.12 (5 lb. dry matter/lb. N). Responses of this level or below it are only likely to be found when light dressings are made on clover-rich swards (see p. 43), or in extremely dry conditions. On clover swards, moreover, the effect of nitrogenous fertilizer in altering the seasonal distribution of herbage growth without necessarily increasing annual yield can be beneficial, although its economic effect is difficult to assess.

Throughout any consideration of the economics of increasing grass production the conflict between fertilizer and clover nitrogen is apparent. The crux of the matter is that reliance on clover imposes a ceiling on production per acre which in this country can be exceeded with the intensive use of nitrogenous fertilizer at little extra cost per unit of food. (See, for example, costs of grass production for

artificial drying Holmes 1954*a*) Circumstances which may justify liberal use of fertilizers are found for example, on small, heavily stocked grassland dairy farms where every effort must be made to increase turnover in order to secure an adequate annual income for the farmer But on bigger farms especially in dry districts there may be less need for the intensive use of nitrogen and in many circumstances profitable increases in production can be achieved simply by improvement in the management and utilization of grass–clover swards

UTILIZATION OF THE EXTRA GRASS

It is most important to consider any intensive programme of improvement in grassland management in terms of its effect on the economy of the farm as a whole because these programmes may demand additional capital investment and expenditure on labour, machinery and livestock. It has been shown in recent years that in commercial dairy farming allowing for all these costs a general increase in fertilizer usage coupled with good grassland management increased profitability partly by reducing the costs of feeding per animal but mainly by increases in stock-carrying capacity and output per acre (Clark and Bessell 1954 1956) These and other studies show that the most common practice is to use improved grassland production to increase the stocking rate rather than to reduce the amount of concentrate feed purchased In the surveys referred to above the amounts of nitrogenous fertilizer used by farmers and the consequent increases in stock-carrying capacity were relatively small and experimental results suggest that much greater increases are possible For example, Holmes (1954*b*) showed that for a dairy herd the stock-carrying capacity of land might be expected to increase from 3 9 acres per cow-equivalent under the traditional methods of management to 1·9 acres under highly intensive methods of management and fertilizer usage, and results from commercial dairy farms now indicate that the higher levels can be profitably achieved and even exceeded The dairy cow is more efficient than beef cattle or sheep in converting animal to human feed (Leitch and Godden 1941) and it is probable that such highly intensive systems of grassland production may be more profitable and normally justifiable only in dairy farming (see also Chapter 10)

Not all farmers are able or willing to find the capital that may be required to increase the number of stock carried, but these farmers may still increase their profits by devoting a smaller acreage to the livestock

enterprise and growing more crops. Another alternative is to use increased and better grass production to reduce the costs of feeding. For example, it has been shown recently by Holmes and Sykes (1960) that liberal feeding of supplementary concentrates to cows grazing in summertime may reduce profit per cow considerably.

In winter feeding less precise information is available although recent milk cost data show that those herds deriving a greater proportion of their feed from grassland gave similar yields and higher profits compared with herds fed in the traditional manner (Ministry of Agriculture, etc., 1960). With beef cattle, Dodsworth and Campbell (1953) have shown that good-quality grass silage can provide a profitable fattening ration.

Accordingly there has been a trend for grass silage to replace some of the root crops in arable cattle fattening areas and for silage to be more widely used except where cheap arable by-products are available.

Arable by-products may also be used in dairying, but in general the question in dairying is not so much whether grass can profitably replace other crops (which, except for these by-products and kale at certain times of the year, is generally accepted) but to what extent a mainly grass ration can be used to reduce the amount of concentrates fed. An increase in the amount and quality of grass feeds can reduce the amount of concentrates required and may increase the profitability of milk production even if milk sales are reduced (Holmes, Arnold and Provan, 1960). If yields fall seriously then an increase in stocking rate becomes essential to maintain profitability. In general, maximum yields per cow cannot be maintained on grass feeds alone, and for the most economic level of production and satisfactory milk quality, some concentrates are necessary; but in many circumstances good silage and hay can provide for maintenance and 1–2 gallons of milk with a consequent reduction in concentrate consumption. The two extreme policies in dairying are: either to increase stocking rate by increased grass production and utilization with low feeding costs but moderate yields; or to raise yields (and to some extent stocking rate) by intensive concentrate feeding with an increase in turnover which justifies the increased costs of feeding. Both methods can be equally profitable provided each gives the levels of production expected of it (Barnard, 1958). In practice, however, it is apparent that, of the two, to increase the stocking rate and the amount of grass fed is the more certain to achieve the result intended because relatively few farmers who feed

high levels of concentrate succeed in achieving anything near a proportionate increase in milk production A survey of national milk records conducted some years ago (Milk Marketing Board, 1952) showed a tendency for yields and profits to increase as the level of concentrated feeding increased between farms, but when the individual herds were classified into groups according to level of yield it was plain that in any one level of yield there were very substantial differences in the amount of concentrates used, and higher profits were made by those farmers who fed the least concentrates A similar lack of relation between yield per cow and level of concentrate feeding on different farms has been reported more recently by the Milk Marketing Board (1959) For the individual farmer the conclusion is that it may pay to increase the level of concentrate feeding provided the quality of the cows and his management of the cows are such that a worth-while response of milk yield can be achieved But he should first satisfy himself that improvements in management of the grassland and the cows would not bring any further increase in yields without recourse to concentrates

It was pointed out above that the dairy cow is more efficient than beef cattle and sheep in converting animal feeds to human food, and by the same argument the latter animals are less likely to justify expensive feeding methods, although this generalization is subject to fluctuations in the prices of concentrates and of meat and milk

Finally, it is important to note that whatever policy is decided on concerning the profitability of using concentrates, increases in the production and utilization of grass on the farm result in increased profitability (Committee on Grassland Utilization, 1958) Grass and concentrate feeds are then complementary since good grass lays the foundation for any subsequent increase in the intensity of feeding

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CHAPTER THREE

Pasture Chemistry

W S FERGUSON

Introduction—Nitrogenous compounds proteins, non-protein nitrogen—Carbohydrates, monosaccharides, oligosaccharides fructosans cellulose, hemicelluloses, pectic substances—Lignin—Lipids—Organic acids—Pigments—Vitamins and minerals

The object of this chapter is to discuss the information available on the true chemical constituents of grassland herbage As will be seen, our knowledge of the chemical identity of many of the constituents, and how the constituents are influenced by the numerous factors influencing plant growth, is lamentably lacking Advancement of knowledge in these directions must lead to a better understanding, and assessment, of the nutritive value of herbage, at least of herbage at a young stage of growth With more mature herbage the matter is more difficult and it does not follow, for example, that a figure for lignin content will necessarily enable us to forecast the degree of locking-up of nutrients brought about by 'lignification'

Grassland herbage, whether intended for grazing or conservation, generally consists of a mixed population of herbage plants with varying growth habits The population, moreover, can be changed by frequency and intensity of grazing or cutting, by climatic conditions and fertilizer treatment (see Chapter 4) It is not surprising, therefore, that there is no constancy in the chemical composition of pasture

In most of the work done on the chemical composition of herbage plants a scheme of analysis has been used which was first suggested about one hundred years ago by Henneberg (1860) Although

inadequate from the chemical view, this analysis, so suitable for routine examinations of large numbers of samples, has yielded valuable information on plant composition. Moreover, in conjunction with animal digestion trials it has formed a sound basis for assessment of the nutritive value of animal foods.

Briefly, the analysis determines the ash content, representing the inorganic constituents, the ether extract or the fats and fat-soluble constituents, the protein (nitrogen content $\times$ 6·25) and the fibre. The nitrogen-free extractives are then calculated by difference.

None of these fractions represents true constituents, as will be seen later, but the main objections are levelled against the fibre and nitrogen-free extractives fractions. The fibre is determined by an empirical method, by subjecting the dry, ether-extracted material to alternate digestion with 1·5 per cent sulphuric acid and 1·25 per cent sodium hydroxide at boiling point for half an hour. As the word implies this was presumed to represent the 'fibrous' portion of the plant. It has been shown, however, that this includes most, but not all, of the cellulose, a portion of a pentose polysaccharide and a part of the lignin of the plant material. Moreover, the relative proportions of these constituents in the fibre vary with different types of forage and very probably with slight variations in analytical procedure. The nitrogen-free extractive fraction consists of a complex mixture of all constituents not determined by the analysis mentioned above. It includes simple sugars, a number of polysaccharides, pectin, organic acids, lignin and a host of other substances in small amounts. It is obviously desirable that this mixture should be separated by other analytical methods. It is of particular importance that lignin, which has such an influence on the digestibility and nutritive value of a crop, should be determined separately. Many workers interested in the nutritive value of fodders now determine cellulose and lignin in addition to protein, ash and ether extract and call the undetermined portion carbohydrates. Others have separated the carbohydrate constituents by water extraction followed by hydrolysis with graded strengths of acid. Another method which may prove useful for the examination of the carbohydrates associated with the structural framework of the plant is the analysis of the 'holocellulose' fraction (Wise, Murphy and D'Addicio, 1946). This fraction, according to workers on the chemistry of wood, represents the structural carbohydrates freed of soluble constituents, protein and lignin, and is obtained by treatments with acidified chlorite solutions. Unfortunately with dried herbage the

number of treatments necessary to remove all the lignin and protein causes some loss of polysaccharides

Ferguson (1948) has used an analysis which determines ash, crude protein, ether extract, water-soluble carbohydrates, organic acids, pectin, cellulose, lignin and pentose polysaccharides Applied to young high-protein grass this analysis accounted for 95 per cent of the herbage dry matter but in more mature grass and hay the recovery was only about 84 per cent The omission of the determination of hexose polysaccharides would partly account for the incomplete recoveries This type of analysis is too laborious for general application in the agricultural field where a more simple approximate analysis would suffice

In the following necessarily brief discussion of the true chemical constituents of grassland herbage the wide field has been dealt with as outlined below

Nitrogenous compounds
- (1) Proteins
- (2) Non-protein compounds—peptides, amino acids, amides, purines, pyrimidines, nitrate, cyanogenetic glycosides

Carbohydrates including pectin
- (1) Non-structural—hexoses, oligosaccharides, fructosan
- (2) Structural—cellulose, hemicelluloses, pectin

Lignin

Lipids

Fats, waxes phosphatides, sterols

Organic acids

Pigments

Chlorophylls carotenoids

Vitamins and some other minor organic constituents

Vitamins D, C E vitamin B complex, coumarin, saponins oestrogens

Minerals

THE NITROGENOUS COMPOUNDS

THE PROTEINS

The proteins of pasture herbage consist of a complex mixture which it is not yet possible to resolve Most of the knowledge gained to

date on the chemistry of the proteins has been derived from studies of the total cell protein, the protein utilized in the nutrition of the grazing animal.

Within the plant cell, proteins are found in a soluble form in the cytoplasm and as particulate matter in the chloroplasts. The proportions in the two forms appear to vary with plant species and, although little information is available, probably some 40 per cent of the total protein of pasture plants is present in the chloroplast fraction.

Even when the semi-permeability of cell membranes is destroyed by cytolysis with ether so that low molecular weight constituents can be extruded through the cell walls by moderate pressure, the cell walls still act as an ultra-filter preventing passage of protein (Chibnall, 1939). For the extraction of the protein the cells must be ruptured by mechanical means and the yield of protein is dependent, therefore, upon the number of cells broken open. Unfortunately, with the machines available for large-scale work, fine maceration is difficult and the efficiency of extraction is consequently frequently very low.

The green extract obtained by coarse filtration of the macerated plant tissue contains cytoplastic and chloroplastic proteins. The latter, in a colloidal state, can be separated by centrifuging, fine filtration or by flocculation with salts. The former, in a clear brown solution after the removal of the chloroplasts, is precipitated by acidification.

The cytoplastic protein obtained by precipitation is usually relatively pure, containing about 14–16 per cent nitrogen and small amounts of inorganic salts, lipids and other organic matter. The chloroplastic protein fraction, however, contains much lipid material, appreciable quantities of salts and organic material in quantities which depend upon the fineness of maceration of the original herbage and the efficiency of removal of cell debris prior to precipitation of the protein. The nitrogen content of the crude chloroplastic fraction is unlikely to exceed 10 per cent and may be much lower. The lipids, which can be removed by ether extraction, may account for some 30 per cent of the fraction and consist mainly of glycerides, waxes and chlorophyll with small quantities of sterols, carotenoids and phosphatides.

By cytolysing the plant cells of grassland herbage with an ether-water mixture the relationship between protein and lipids in the chloroplasts is altered and the protein becomes soluble or easily dispersed in the aqueous extract. The total cell protein can then be precipitated by acidification.

For the preparation of total leaf protein Lugg (1939) recommends

maceration of the plant with borate buffer solution (pH 9.2). After a rough filtration an alcohol-ether mixture is added to the green, opaque juice, thus precipitating remaining cell debris and disintegrated particulate matter of the cells. After centrifuging, the protein is precipitated by acidification to pH 4.5 and heat. The protein, after extraction with alcohol and ether, is reasonably pure and should contain about 14 per cent nitrogen.

Since it is difficult to break open the cells of pasture plants by mechanical means, protein preparations yield only a proportion of the total leaf protein and protein analyses have been made on preparations forming as low as 10 per cent of the total protein. It is probable that the protein extracted from pasture plants is a representative fraction of the whole although this may not be so with other species. Determinations of certain amino acids in the total herbage, in the extracted protein and in the fibrous residue remaining after extraction, support this view.

Comparative amino acid analyses of cytoplastic and chloroplastic proteins from pasture plants are not available but figures for prepara-

TABLE 3.1 *Amino acid content of barley leaf protein* (Yemm and Folkes, 1953)

	Amino N as % of protein N		Amino acids as % of protein (17% N)	
	Mixed proteins	Cytoplasmic proteins	Mixed proteins	Cytoplasmic proteins
Alanine	8.0	7.9	8.65	8.53
Amide	4.8	4.8	4.05	4.05
Arginine	15.0	15.0	7.92	7.92
Aspartic acid	6.6	6.4	10.66	10.34
Cystine + cysteine	0.9	0.9	1.31	1.31
Glutamic acid	8.2	8.2	14.64	14.64
Glycine	6.5	6.7	5.92	6.10
Histidine	4·0	4.1	2.52	2.57
Leucine	5.8	5.9	9.23	9.38
Isoleucine	4.7	4.2	7.48	6.68
Lysine	6.5	7.1	5.76	6.29
Methionine	1.3	1.4	2.33	2.52
Phenylalanine	3.2	3.0	6.41	6.02
Proline	4.0	4.1	5.59	5.73
Serine	3.3	3.5	4.20	4.45
Threonine	4.0	4.0	5.78	5.78
Tryptophane	1.8	2.0	2.23	2.48
Tyrosine	2.2	2.4	5.27	5.75
Valine	5.0	4.9	7.11	6.95

tions containing varying proportions of the two proteins show close similarity. A comprehensive examination of the mixed and cytoplastic proteins of barley leaves has shown (Table 3.1) a remarkable similarity in amino acid composition (Yemm and Folkes, 1953). Chloroplastic protein was also prepared but this was too contaminated with non-protein organic material for accurate amino acid analysis. In this work the amino and amide nitrogen, determined mainly by microbiological methods, accounted for practically all the nitrogen in the protein and it was calculated that the pure protein had a nitrogen content of 16·9 per cent. Other workers have reported similar values for proteins of pasture herbage and it seems that the factor of 6·25 generally used to convert nitrogen to protein is too high for leaf protein and a better factor would be 5·9 or 6·0.

Much early work on the amino acid composition of pasture protein is suspect owing to amino acid destruction during hydrolysis of impure proteins and inadequate analytical methods. Further work with modern techniques is needed to fill the gaps in our knowledge. Authoritative workers in the field consider that all leaf proteins have, within reasonable limits, very similar amino acid composition and that this is not markedly affected by season, stage of growth or manurial treatment.

Lugg (1949), using data from many sources, has compiled a table showing the range of variation in amino acid compositions of the total leaf proteins from Leguminosae and Gramineae. Seven legumes were considered, mainly clovers but runner bean leaves were included. The Gramineae included most of the common grasses. The figures given in Table 3.2 do not necessarily indicate the full range of amino acid compositions since they are compiled from an inadequate number of samples. They do indicate, however, the approximate composition, and the range may not need to be modified except for a few amino acids.

The relative constancy of leaf proteins has been questioned by Smith and Agiza (1951) who examined the proteins of a number of pasture species at various stages of growth. By chromatographic methods they found that the proportions of amino acids were affected by several factors. As growth proceeded through the vegetative period to seed formation aspartic and glutamic acids increased but arginine and lysine decreased. Several other acids displayed regular trends but not in all species. There was a seasonal effect, samples from the first growth of herbages invariably containing more leucines and arginine, and less

TABLE 3.2. *Amino acid contents of total leaf proteins* (Lugg 1949)

	Amino N as % of protein N		Amino acids as % of protein (17% N)	
	Leguminosae	Gramineae	Leguminosae	Gramineae
Alanine	–	4 4 5 1	–	4 75–5 51
Amide	5 1–5 3	4 7–5 3	4 30–4 47	3 97–4 47
Arginine	13 0–14 0	13 7–14 3	6 87 7 40	7 24–7 55
Aspartic acid	4 7 5 4	4 9–5 4	7 59–8 72	7 91–8 72
Cystine+cysteine	1 1–1 3	1 3–1 5	1 60–1 89	1 87–2 19
Glutamic acid	6 4–6·7	6 6–7 8	11 42–11 9[illegible]	11 78–13 92
Glycine	–	0 4	–	0 36
Histidine	3 8 4 0	3 6–3 7	[illegible] 38 [illegible] 51	2 [illegible]6–2 3[illegible]
Leucine	7 3	7 1 8 8	11 61	11 29–14 00
Isoleucine	3 6		5 73	
Lysine	6 4–6 5	6 3–6 6	5 67 5 76	5 58–5 85
Methionine	1 2–1 4	1 4–1 6	2 16–[illegible] 52	2 52–2 88
Phenylalanine	2 4	2 5 2 6	4 81	5·01–5 21
Proline	–	3 1	–	4 33
Threonine	4 0	3 0	5 78	4 34
Tryptophane	1 6–1 9	1 8–2 1	1 98–2 35	2 23–2 60
Tyrosine	2 3–2 6	2 3–2 5	5 50–6 22	5 50–5 98
Valine	4 5	3 3–4 2	6 39	4 69–5·97

glutamic acid than the second growth Within grass and clover species differences in amino acid composition were noted even when the herbages were cut at the same stage of growth or age Nitrogenous fertilizers decreased aspartic and glutamic acid and increased leucines, phenylalanine arginine lysine and tryptophane in young ryegrass and red clover but it was not clear if this was due to an increase in leafiness and nitrogen content of the plants or to a prolongation of the vegetative period Arginine and lysine were also increased in hay by a late application of nitrogenous fertilizer

This work has been criticized by Waite, Fensom and Lovett (1953) on the ground that the method used for the hydrolysis of the protein may not have been rigorous enough to break down the more impure proteins and consequently some of the figures for arginine and lysine could be low These workers examined proteins isolated from ryegrass meadow fescue timothy and cocksfoot the herbages being cut at a young stage of growth in spring summer and autumn and also at a more mature stage in the autumn Only the basic amino acids were determined and these varied little despite differences in stage of growth of the herbages or season of cutting Even between species

no marked differences were seen although cocksfoot appeared to have a slightly lower lysine content than the other three grasses. A summary of the figures is given in Table 3.3.

TABLE 3.3. *The basic amino acid content of grass proteins* (Waite *et al.*, 1953)

% of protein containing 16% nitrogen

	Lysine	Arginine	Histidine
Ryegrass	5·9 (5·3–6·4)	7·5 (6·6–8·2)	1·5 (1·1–1·8)
Meadow fescue	6·3 (5·8–6·9)	7·0 (6·1–8·0)	1·3 (1·2–1·6)
Timothy	5·7 (5·0–6·5)	6·9 (6·2–7·5)	1·5 (1·3–1·7)
Cocksfoot	5·2 (4·7–6·3)	7·7 (6·8–8·6)	1·4 (1·2–1·7)

Kemble and Macpherson (1954) determined the monoamino monocarboxylic acid contents of protein preparations of ryegrass, mixed herbage from permanent pasture, lawn grass and Alsike clover. The plants differed in stage of growth but the amino acid compositions were remarkably similar (Table 3.4). The protein from wilted grass gave similar figures even although appreciable proteolysis occurs during wilting.

TABLE 3.4. *Monoamino monocarboxylic acid content of herbage proteins* (Kemble and Macpherson, 1954)

Amino N as % protein N

	Grasses	Wilted grass	Alsike clover
Alanine	5·7–5·9	5·8	5·9
Glycine	6·4–6·9	6·9	7·0
Leucine	5·3–5·9	5·3	5·7
Isoleucine	3·3–3·4	3·4	3·5
Phenylalanine	3·5–3·6	3·5	3·3
Proline	3·5–3·7	3·6	3·8
Serine	4·0–4·2	4·0	3·9
Threonine	4·3–4·5	4·2	4·2
Tyrosine	1·5–1·7	1·6	1·6
Valine	4·4–4·8	4·5	4·7

The figures for the monoamino monocarboxylic acids, except isoleucine and alanine, are close to those found in barley leaf protein

(Table 3 1) and are higher than those quoted by Lugg (Table 3.2), the exception being tyrosine which may have been underestimated by Kemble and Macpherson

In a study of the amino acid composition of hays Kolousek and Coulson (1955) suggest that composition is affected during the hay-making process and that the actual stage of growth or the species of grass may affect the composition wherever changes do take place Tyrosine, methionine, phenylalanine, proline and glycine are the acids mainly affected, the basic amino acids are less affected and the remainder show little, if any, changes The glycine contents were similar to those found by Kemble and Macpherson and very much higher than those quoted by earlier workers

From this summary it is obvious that our knowledge of the amino acid composition of pasture protein is very inadequate and further investigations, using modern techniques are desirable to see what variations arise in different herbage species and how they are affected by stage of growth, conditions of growth and fertilizer treatments It seems probable, however, that no very remarkable variations will be found and a more important problem is to decide to what degree amino acid composition of proteins is of significance in the nutrition of the grazing animal

Pasture protein is a useful source of most of the amino acids found to be essential in non-ruminant nutrition This fact has been realized and efforts made to prepare economically from grassland herbages a protein concentrate for inclusion in pig poultry and even human diets In the ruminant, rumen micro-organisms modify the nutritional value of nitrogenous substances in the ration, by food-protein breakdown and build-up of bacterial and protozoal protein Although the proportion of dietary protein converted in this way is not known with certainty, it is appreciable The proteins of the micro-organisms, which are digested by the host, are of high biological value and it seems probable therefore that the biological value, or content of essential amino acids, of the proteins fed to ruminants for body maintenance and growth is of relatively little importance In high-producing animals, particularly cows yielding large quantities of milk, the position may be different and such animals may depend on ingested essential amino acids for the production of milk proteins

It has been suggested that dietary lysine and possibly tryptophane might be limiting factors in milk production, and also factors influencing the apparent difference in feeding value of spring and autumn

pastures. Pasture analyses, however, have failed to substantiate these suggestions. The possibility that the sulphur-amino acid content of feeds might limit wool production in sheep has received attention and the position is still not clear. In general on good-quality pasture the intake of protein by the grazing animal well exceeds its requirements and the excess would help to balance the supply of any essential amino acids which might be present in low concentrations.

THE NON-PROTEIN NITROGENOUS CONSTITUENTS

The non-protein nitrogenous fraction of herbage plants is made up of an extremely complex mixture of compounds. Our knowledge of this fraction is limited mainly owing to the difficulty of separating the constituents. By modern methods of chromatography and ionophoresis, useful separations of many of the constituents can now be made and a widening of our knowledge should follow.

Compounds concerned in protein metabolism—nitrate, ammonia, amino acids, acid amides and peptides—account for the major part of the fraction, the rest consisting of purine bases, simple bases such as betaine, stachydrine and choline, and possibly numerous compounds in trace amounts. The fraction usually accounts for 15–25 per cent of the total plant nitrogen but the proportion varies with rate and stage of plant growth. It is reasonable to assume that in young, rapidly growing herbage the production of non-protein nitrogenous constituents is higher than in herbage where growth is limited by age or other factors.

Synge (1951), from work on dialysed juice of perennial ryegrass, has made the following rough quantitative estimate of the constituents of the non-protein nitrogenous fraction.

	Nitrogen, as % of total diffusable N
Non-amino acid bases	15–25
Basic amino acids, peptides, etc.	6–15
γ aminobutyric acid	5–10
Glutamine	20–25
Other free neutral amino acids	10–15
'Bound' amino acids in neutral compounds	4–10
Free glutamic and aspartic acids	10–20
'Bound' amino acids in acidic compounds	1–3

It is seen that amino acids, amides and peptides account for 75–85 per cent of the diffusable nitrogen.

Some twenty free amino acids have been determined in herbage

extracts Their quantitative pattern is very different from that found in herbage proteins, the bulk consisting of the dicarboxylic acids and their amides, alanine, serine and γ aminobutyric acid The relative quantities of these amino acids vary with the stage growth of the plant and may be influenced, in early stages of growth, by different forms of fertilizer nitrogen

Bathurst (1953) examined the amino acid content of alcoholic extracts of very young perennial ryegrass which had been topdressed with ammonium sulphate, sodium nitrate or urea The amino acids were assayed *microbiologically* and the results are shown in Table 3 5 The main differences noted here are the greater quantities of proline and aspartic acid (including asparagine) in the ryegrass dressed with ammonium sulphate

and other amino compounds, not yet satisfactorily identified, have been noted in lucerne hay (Coulson, 1955).

It has been shown that herbage allowed to wilt, or herbage dried in laboratory ovens, rapidly undergoes proteolysis, with a consequent increase in the quantity of water-soluble nitrogenous constituents, and also suffers changes in ammonia and amide contents. Investigations on the non-protein nitrogenous fraction should, therefore, be carried out on fresh herbage or on material that has been freeze-dried, a process which minimizes proteolysis.

In agricultural circles so-called 'true protein' is determined on dried herbages by precipitation with a copper reagent. Since drying conditions, and consequently proteolysis, vary considerably and also since it is not known to what extent peptides and amino acids are precipitated by the reagent, there seems little justification in making this determination.

Many peptides and 'bound' amino acids are present in the non-protein nitrogenous fraction. In general their amino acid composition is markedly different from the pattern of free amino acids, the dicarboxylic acids being in smaller, and the basic amino acids in larger, proportions. By ionophoretic fractionation of the diffusable constituents of ryegrass it has been shown that basic, acidic and neutral compounds are all present and that the neutral ones form the greatest part of the total. These neutral compounds give only a few amino acids on hydrolysis, mainly leucine-isoleucine, valine, proline, alanine, glycine and the dicarboxylic acids and their amides (Synge, 1951).

Four purines, adenine, guanine, xanthine and hypoxanthine have been noted in grass and lucerne extracts, adenine preponderating in quantity (Ferguson and Terry, 1954). In the three grasses and one lucerne examined the total purine nitrogen varied from 45 to 67 mg. per 100 g. herbage dry matter. In the same herbages the quantities of betaine nitrogen and choline nitrogen did not exceed 17 mg. per 100 gm. dry herbage. Small quantities of pyrimidines and presumed nucleotides were also noted.

Nitrate nitrogen can form an appreciable part of the non-protein nitrogenous fraction under certain circumstances. The level is greatly influenced by the quantity of available nitrogen in the soil and rapidity of plant growth. In Holland, where urine as well as dung is returned to pasture-land and usage of fertilizer nitrogen is relatively heavy, herbage samples taken at various times from 'average' farms showed a mean nitrate nitrogen content of 55 mg. per 100 gm. herbage dry matter,

range 3–180 mg On a very intensive farm using large amounts of fertilizer nitrogen the mean value was 132 mg with a range of 22 to 358 mg (Deijs, 1953) Under very generous nitrogenous manuring the nitrate level in herbage shows a seasonal trend, being moderately high in early spring growth, negligible in midsummer and rising to a maximum in the autumn (Ferguson and Terry, 1956)

Cyanogenetic glycosides may be considered with the non-protein nitrogenous constituents They are insignificant constituents of the common cultivated pasture grasses but the sorghums and Sudan grass can contain appreciable, and sometimes toxic, amounts They are present in legumes and the quantity of hydrocyanic acid (HCN) in the glycosides of white clover would, at times, be toxic if it were in a free state An examination of the HCN content of a number of pasture species showed that grasses contained 0 0001–0 0005 per cent, red clover 0 0003 per cent, lucerne 0 0015 per cent and white clover 0 0016–0 0124 per cent (Rigg, Askew and Kidson, 1933), the figures being expressed on fresh herbage Two cyanogenetic glycosides occur in white clover, lotaustralin, consisting of units of glucose, methyl-ethyl ketone and HCN, and linamarin, made up of glucose, acetone and HCN Using fresh white clover containing between 0 015 and 0 025 per cent HCN, Melville and Doak (1940) found the glycoside mixture contained 80 per cent lotaustralin and 20 per cent linamarin These glycosides contain 10 3 per cent and 10 9 per cent HCN respectively and about 70 per cent glucose The glycosides are readily hydrolysed by the enzyme linamarase which occurs with varying frequency in different strains, and even within strains, of white clover The quantity of glycoside present in white clovers, as measured by HCN content, varies markedly in different strains, and even within strains individual plants show wide variations In New Zealand the HCN content of white clover has been used for strain certification purposes since it is considered that the high-quality persistent strains contain more glycoside than less desirable ones

THE CARBOHYDRATES, INCLUDING PECTIN

NON-STRUCTURAL CARBOHYDRATES

Monosaccharides The hexoses, *glucose* and *fructose*, form only a small part of the carbohydrates of herbage, each contributing up to 2 per cent of the herbage dry matter The minor changes due to season and stage of plant growth will be discussed later

Oligosaccharides. In herbage, *sucrose* is usually present to the extent of 5–6 per cent and the quantity is influenced by growing conditions and stage of plant growth. The presence in grasses of small amounts of the disaccharide *mellibiose*, the trisaccharide *raffinose* and the tetrasaccharide *stachyose* has been noted (Laidlaw and Reid, 1952).

Fructosan. In grasses, fructosan is a reserve carbohydrate which is formed in the leaves but does not accumulate there to any great extent, being stored in the stems. It shows remarkable seasonal variation which is dealt with below. It is of interest that no fructosan has been detected in clover or lucerne.

The fructosan of grasses probably has a structure represented by a chain of some 7–30 D-fructofuranose units linked through $C_{(2)}$ and $C_{(6)}$ and it is suggested that the molecule is terminated by a sucrose molecule (Laidlaw and Reid, 1951).

Variations in the hexose, sucrose and fructosan contents of grasses. Waite and Boyd (1953) have made a comprehensive study over two years of the hexose, sucrose and fructosan contents of four grass species in stages from early spring growth to autumn senescence and also in the grasses cut at a constant height (8–10 in.) regularly throughout the grass season, the latter representing herbage as grazed by cattle. The grasses were perennial ryegrass, cocksfoot, meadow fescue and timothy. Sugar analyses were made on both leaf and stem and all the figures given below refer to sugar content of herbage dry matter.

In the grasses growing to maturity, leaf hexose levels were low and similar in all species, 2 per cent or less throughout the period April to October. Leaf sucrose usually rose to a maximum, 5–6 per cent, in May and June and then declined steadily. Ryegrass differed in that it showed maxima of 8 and 11 per cent sucrose in the two years. Leaf fructosan varied markedly in the two years, timothy and fescue containing maxima of 11 per cent in one year and 3 per cent in the other, ryegrass 16 and 11 per cent and cocksfoot 9 per cent in both years. Hexoses in the stems were present in small quantity, although greater than in the leaf, but showed a marked rise in early June, except in the case of ryegrass. Stem sucrose showed about the same level and trends as the leaf sucrose. Some very high figures were recorded for stem fructosan, the maxima being 34 per cent in timothy, 32 per cent in ryegrass, 26 per cent in cocksfoot and 23 per cent in fescue. In fescue, timothy and cocksfoot the fructosan showed two peaks although the levels differed in the two years. Ryegrass fructosan was similar in both years, showing only one peak in June. It is suggested that the

store of fructosan in the stems is depleted by the heavy demands made by the rapidly elongating growing point and again when seed is being formed The fructosan level in the plant is evidently affected by growth habit and season In early-flowering species when rapid growth is encouraged by a warm early spring there may be little opportunity for a build-up of a substantial reserve of fructosan In late-flowering species the fructosan content is apparently less affected by weather conditions early in the year

In the study of the seasonal variations of sugars in the grass species cut at the grazing stage the grasses were cut at a height of 8–10 in leaving a 1–2 in stubble Cutting was done between 9 and 10 a m The grasses received potash and phosphate fertilizers in February of each year and generous applications of nitrogenous fertilizer throughout each grass season The hexose, sucrose fructosan and total soluble sugar contents of the four species over two years are given in Table 3 6 The figures show that the total sugar contents up to mid-

TABLE 3 6 *Soluble carbohydrate and crude protein contents of grasses at the grazing stage* (Waite and Boyd 1953)

% of dry matter

Grass	Date cut	Hexoses	Sucrose	Fructosan	Total soluble sugars	Crude protein
	1951					
Ryegrass	15 June	1 9	5 4	16 1	25 5	8 3
	12 July	1 0	3 5	4 6	9 1	16 9
	27 July	1 5	2 8	1 4	6 0	24 9
	15 Aug	1 9	4 5	0 5	7 2	26 1
	30 Aug	1 4	4 7	0 7	7 1	25 3
	18 Sept.	1 0	3 9	1 1	5 8	24 3
Timothy	18 June	1 8	3·9	9 3	16 3	8 4
	17 July	1 0	3 9	1 4	6 7	16 9
	20 Aug	1 7	5 9	5 8	14 3	14 6
	17 Sept.	0 8	3 9	0 6	5 6	21 9
Fescue	17 May	3·0	10 3	11 6	26 3	15 0
	8 June	3·9	7 4	7 7	20 3	11 8
	28 June	1 8	3 7	6 9	11 9	16 3
	12 July	1 1	2 0	1 1	4 3	25 7
	27 July	1 6	2 0	1 1	5 0	24 4
	14 Aug	1 6	5 6	0 6	8 2	25·0
	28 Aug	2 2	5 5	0·7	8 8	26 4
	2 Oct.	1 2	3 2	2 3	7 2	21 6

TABLE 3.6.—*continued*

% of dry matter

Grass	Date cut	Hexoses	Sucrose	Fructosan	Total soluble sugars	Crude protein
	1951					
Fescue—*con.*	15 June	2·0	4·5	10·7	18 6	8·0
	8 July	0 9	3 6	0·8	5·9	20·2
Cocksfoot	24 July	1·5	5·0	0·9	7·7	22·9
	15 Aug.	1·0	3·4	0 9	5·5	24·7
	30 Aug.	0·7	2 8	0·3	4·0	29·2
	17 Sept.	0 5	3·5	0·2	4·4	30·6
	1952					
	20 May	2 9	5·0	9 0	17·9	14·1
	25 June	1·7	5·4	12·7	21·6	14·4
Ryegrass	11 July	1·3	2·3	0 9	4·6	26·4
	29 July	2·6	6·7	2·6	12·4	23·0
	4 Sept.	1·7	4·7	4·0	11·6	16·5
	21 Oct.	1·6	6·9	3·0	12·1	20·3
	12 May	1·8	4·8	5·7	12·7	18·1
	24 May	2·5	6·4	0·7	9·8	22·6
	19 June	1·4	5·1	3·8	11·0	19·1
Timothy	12 July	1·3	3·6	0·5	5·5	21·8
	29 July	1·7	5·8	0·3	8·2	25·2
	21 Aug.	1·3	4·4	0·3	6·3	25·2
	30 Sept.	0·9	6·1	1·0	8 9	21·1
	28 Apr.	1·9	5·3	2·9	10·3	24·8
	20 May	2·0	3·8	2·4	8·5	18·1
	19 June	1·8	6·2	5·2	14·0	18·5
Fescue	3 July	0·9	5 0	0·4	6·6	26·1
	22 July	0·9	2·3	0·2	3·5	25·6
	20 Aug.	1·1	3·5	0 8	5·8	23·1
	29 Sept.	1·1	5·6	1·9	9 3	19·2
	7 May	2·1	4·3	2·4	9·1	20·9
	22 May	0 9	3·5	0·5	5·0	25·6
	13 June	1·1	3·9	0·4	5·6	24·4
Cocksfoot	2 July	0 8	1·6	0·0	2·6	26·4
	22 July	0·9	1·0	0·1	2·0	24·9
	20 Aug.	0·3	2·1	0·1	2·7	23·0
	29 Sept.	1·1	3·3	1·0	5·8	18·5

June, when the grasses were developing floral growing points, were high but after this date, when growth was vegetative, the level was low. The change was due essentially to the fructosan content, the hexose

and sucrose values showing only small irregular changes After June fructosan was no longer the most plentiful sugar in the herbage Marked differences between species in sugar content seem apparent but the effect of weather conditions is even more marked particularly early in the season the early warm spring of 1952 producing lower fructosan levels than the colder spring of 1951

The grasses in this investigation were encouraged to grow rapidly by the generous use of fertilizer nitrogen and this is reflected in the high protein content of the samples taken after June, very few showing less than 20 per cent crude protein Later Waite (1958) concluded that a stimulating effect of fertilizers resulted in the utilization of sugars for leafy growth at the expense of carbohydrate in the form of fructosan Norman (1939) had reported a slight lowering of the fructosan content of first-growth cocksfoot by nitrogenous manuring but this was less evident in the second growth Whether manured with nitrogenous fertilizer or not, the second growth contained much less fructosan than the first growth

Other workers have noted the high fructosan content of grasses in the early summer and it would seem that ryegrass is outstanding in this regard Waite (1957) determined the water-soluble carbohydrate contents of eight strains of ryegrass of varying rates of growth, two strains of timothy and one strain of cocksfoot in their first and second year of growth In the first year extremely rapid growth and flowering of annual ryegrasses resulted in a much smaller accumulation of fructosan than in the perennial species although the free hexose contents were higher

In the second year an early rise in fructosan content was followed by a marked fall at flower formation in timothy and cocksfoot but not in the ryegrasses During stem elongation after flower emergence the fructosan content of timothy and cocksfoot rose again but that of the ryegrasses fell rapidly

Waite concludes that of the common grasses perennial ryegrasses are most likely to provide a high fructosan content at the growth stages suitable for grazing or ensiling At the hay stage timothy would be expected to be richest in this constituent Cocksfoot, at any height, is likely to contain relatively small amounts of fructosan

Information on the sugar content of clovers is scanty The clovers contain glucose, fructose and sucrose, in smaller amounts than in grasses, but apparently no fructosan. It is likely that another polysaccharide, such as starch, araban or galactan, may be the reserve carbo-

hydrate in legumes, and Bailey (1958) has found 3–5·5 per cent starch in clover leaves. The low soluble-sugar content of legumes offers one explanation why they are more difficult to ensile than grasses. Even in grasses the carbohydrate level influences the ensiling process, a high content of easily hydrolysed fructosan in spring grass ensuring a satisfactory type of fermentation which is frequently lacking when autumn grass, low in fructosan, is ensiled.

STRUCTURAL CARBOHYDRATES AND PECTIN

Cellulose. Cellulose is the major constituent of the cell wall of all plants. Although the structure of the cellulose of herbage has not been studied it is probably similar to other plant celluloses which are glucose-polysaccharides consisting of long chains of glucopyranose units linked through carbon atoms 1 and 4 by β-glucosidic bonds. These chains are packed into well-orientated aggregates, or micelles and microfibrils, which are 'encrusted' with lignin and a range of polysaccharides generally termed hemicelluloses.

The classical method for the determination of cellulose involves treatments with chlorine and sodium sulphite solution which remove all but the cellulosic framework and a xylan fraction. Some workers regard this xylan, or cellulosan, as an integral part of the cellulosic framework of any plant material, although not necessarily chemically combined, or prefer to designate cellulose plus the xylan as 'natural' cellulose. Since the xylan can be removed by treatment with acid or alkali, and other methods for determining cellulose remove varying quantities of the xylan it is more realistic to consider it as one of the hemicelluloses. The determination of 'natural' cellulose might be justified if this cellulose contained a constant proportion of xylan but this does not seem the case. In maturing ryegrass Norman (1936) found the xylan content to increase from 20 to 30 per cent but in a further similar investigation it varied irregularly between 23 and 29 per cent (Norman and Richardson, 1937). In seven grass species cut at a young stage of growth a variation of 8 to 25 per cent was obtained (Buston, 1934).

Cellulose, being the main structural constituent of the plant, forms an increasing proportion of the plant as it matures, and examples of the changes are afforded by work on ryegrass and timothy. In ryegrass (Western Wolths) the true cellulose content increased from 16·8 to 29·0 per cent of the dry matter as the grass matured over a period of 51 days (Norman, 1936). In timothy, the increase was from 21 to

29 per cent in about 50 days (Phillips Davis and Weihe 1942) The range of cellulose contents of herbage grasses is from about 15 to 35 per cent the level being determined mainly by stage of plant growth but also by growth habit and other characteristics of the individual species

The natural cellulose of clovers contains less xylan than that of grasses at least when the plants are young There is a surprising lack of information on the cellulose content of pasture clovers particularly in regard to changes with maturity If however fibre contents are considered fair reflections of cellulose contents then the clovers generally contain less cellulose than the grasses Clovers apparently show little seasonal variation if cut young since in S100 white clover cut four times at the 5–6 in stage from June to September the cellulose content varied only between 13 0 and 15 6 per cent The xylan associated with this cellulose varied from 2 1 to 2 5 per cent In lucerne cut four times about 12 in high the figures for cellulose were 15 3 to 19 8 per cent and for the associated xylan 2 7 to 4 3 per cent

The Hemicelluloses The name hemicelluloses has been given to a group of substances intimately associated with the cellulosic structure of the plant cell wall Hemicelluloses have been defined as cell wall polysaccharides soluble in dilute alkalis but not in water which may be hydrolysed to constituent sugar and sugar acid units by boiling with dilute mineral acids

According to Jermyn (1955) typical hemicellulose preparations may include

(1) Short-chain glucans either removed from the cellulose fibrils by the extraction process or existing outside the fibrils in the encrusting polysaccharides

(2) Polymers of xylose arabinose mannose galactose and possibly other monose units Whether these exist as chains built up of like units or of mixed units is still uncertain in most cases

(3) Mixed polymers of sugar units and uronic acid units usually methylated and sometimes acetylated.

(4) Residual pectin polysaccharides when these have not been completely removed earlier Separation of pectin araban and galactan from hemicellulose araban and galactan is almost always arbitrary

(5) The special polysaccharides which form the bulk of the cell walls of certain plant materials e g the mannan of the ivory nut may be included as hemicelluloses or not purely by expanding or contracting

the scope of definitions Seaweed polysaccharides, although not usually considered as hemicelluloses, are nevertheless extracted and analysed by much the same methods

For the separation of the hemicelluloses a procedure of fractional precipitation from alkaline solution has been widely used The plant material is freed of pectin—and this may not always be easy—and then extracted with hot or cold alkali solution The extract is acidified in steps and the precipitated hemicelluloses recovered Further fractions are obtained by the addition of acetone The method of Norris and Preece (1930), which has been used for the examination of grass hemicelluloses, separates the hemicelluloses into three main fractions hemicellulose A, by acidification of the alkaline extract, hemicellulose B, by the addition of half volume of acetone to the filtrate from A, and hemicellulose C, by the addition of a further volume of acetone to the filtrate from B These are fractionated further by precipitation of hemicellulose-copper complexes, the hemicelluloses obtained from the complexes being termed A, B, and C, and those not precipitated by copper A_2, B_2 and C_2 The hemicelluloses separated in this way cannot be expected to be pure compounds even if relatively few hemicelluloses are present Subsequent work on the identification of the sugar units in the separated hemicelluloses generally reveals a mixture of sugars but no proof of their origin

Buston (1934) examined the hemicelluloses of cocksfoot by the procedure of Norris and Preece The various fractions accounted for only 60 per cent of the total hemicelluloses so the analytical figures may not be truly representative The figures quoted below are means of results obtained in two years

Fraction	Uronic anhydride % ($CO_2 \times 4$)	Furfural %	Units identified
A	1 6	58 4	Almost entirely xylose, with a trace of arabinose
B_1	10 7	52 5	Mainly xylose, 15% arabinose, galacturonic acid
B_2	3 1	16 4	70% hexose, galactose, arabinose
C_1	6 7	53 7	Mainly xylose, 15% arabinose, uronic acid unidentified
C_2	9 9	44 5	50% xylose 24% arabinose, galactose, galacturonic acid

Xylose was the most plentiful sugar and fraction A was evidently almost entirely a xylan Incomplete precipitation of the total xylan in fraction A may be the reason for the appearance of the xylose in some of the other fractions Arabinose was found in all the fractions in varying amounts and galactose in two Galacturonic acid was the only uronic acid identified and the quantity was small, probably amounting to less than 1 per cent of the herbage dry matter

Harwood (1954) has developed a method for the examination of cell-wall polysaccharides which involves a two-stage acid hydrolysis of alcohol and water extracted herbage An analysis of perennial rye-grass of unstated age showed that xylose was the chief sugar present Calculated as polysaccharides the relative quantities of xylan, araban and galactan were 5 1 1 3, the galactan included some glucose presumed to have come from degraded cellulose

Yet another line of attack on the hemicellulose fraction has used delignified cell-wall (holocellulose) as a starting point (Wise *et al*, 1946) Treatment of plant tissue with sodium chlorite in slightly acid solution removes most of the lignin and soluble constituents although extended treatment to remove all lignin can lead to losses of polysaccharides The holocellulose remaining after treatment is fractionated by extraction with alkalis of varying strengths The method has been used widely in investigations on the chemistry of woods but with pasture herbage the delignification is not easy and protein removal is incomplete

Binger, Sullivan and Jenson (1954) examined the hemicelluloses of cocksfoot by this method and separated eight fractions from the holocellulose by hot water and alkali extractions They found that on hydrolysis all fractions contained xylose, glucose, arabinose, galactose and uronic acid xylose accounting for 74 per cent of the total sugars A point of interest is that about 70 per cent of the hemicellulose of the holocellulose was soluble in boiling water

Routley and Sullivan (1958) prepared hemicelluloses from the holocellulose of brome grass (*Bromus inermis*) by extraction with hot water and alkali The water-extractable hemicelluloses contained four sugars two uronic acids and four unidentified substances The sugars were xylose, arabinose, glucose and galactose, xylose being the most plentiful Of the uronic acids, galacturonic was present in greater quantity than glucuronic acid In the alkali-soluble hemicelluloses only xylose and glucose were found

Buston (1934) determined the total hemicellulose content of eight

grass species by the method outlined earlier. Most of the herbages were cut at a young stage of growth but samples of cocksfoot 12 in. high were included. The hemicellulose content only varied from 16·2 to 20·7 per cent of the herbage dry matter, the more mature cocksfoot giving 18·4 per cent. The fraction, therefore, forms a considerable part of the herbage dry matter even in the young plant.

The changes with maturity are illustrated by the work of Bennett (1940) who examined the changes in composition of Kentucky blue grass and red clover. The total hemicelluloses were determined by the method of Buston (1934). Herbage samples were taken when the plants were 3 in. tall and every 5–8 days thereafter to the flowering stage. The analytical data for the first and last samples only are given in Table 3.7.

TABLE 3.7. *Composition of herbage from young stage of growth to flowering* (Bennett, 1940)

Date of sampling	% dry matter Hemicellulose	Pectin	Furfural as pentosan
		Kentucky blue grass	
26 April 1935	14·2	0·7	10·6
27 May ,,	27·8	1·0	20·3
8 May 1936	18·1	0·9	14·8
10 June ,,	25·1	1·1	21·3
16 May 1937	20·4	0·9	16·3
9 June ,,	25·2	0·8	19·9
		Red clover	
8 May 1936	6·9	5·6	8·2
10 June ,,	11·4	5·5	11·2
14 May 1937	4·3	7·2	8·8
20 June ,,	8·5	7·0	11·6

The hemicellulose content increases with age of plant and the grass contains a much higher quantity than the clover. The clover, however, is much richer in the other structural constituent, pectin. The furfural, calculated as pentosan in the Table, is a measure of the pentosans and uronic acids of the hemicelluloses and pectin, and the values illustrate the preponderance of pentose units in the hemicellulose.

Waite (1959) examined the holocellulose fraction of perennial grasses and an annual ryegrass cut at varying stages of growth. As

age increased the contents of xylan cellulosic glucosan and uronic acid rose but the non-xylan hemicelluloses showed only small changes The polysaccharides in leaf and stem were similar Compared with perennial grasses the annual grass contained a smaller proportion of hemicelluloses

From this brief discussion on the chemical nature of the hemicelluloses of pasture plants it is clear that precise knowledge of the constituents is lacking and not likely to be easily attained. Undoubtedly the pentose polysaccharide, xylan, is present but the presence of free araban, galactan and glucosan is uncertain It is thought by many workers that these polysaccharides, and also xylan, are present in the plant structures as definite compounds with a uronic acid. Further experimental work may show if this is true or if the polysaccharides are bound only physically to a polyuronic acid.

Pectic substances Very little is known about the pectic substances of pasture plants In grasses they are minor constituents accounting for up to about 3 per cent of herbage dry matter but clovers may contain appreciably more In a study (Bennett, 1940) of the pectic substances of Kentucky blue grass (*Poa pratensis*) and red clover (*Trifolium pratensis*) harvested from a very young stage of growth to the flowering stage, the highest quantity found in the grass was 1·1 per cent and in the clover, 8 3 per cent No seasonal trend was apparent

In other plants these substances occur particularly in the primary cell walls and also in the middle lamella although they are sometimes found in plant juices They are derivatives of polygalacturonic acid and occur in the following forms (1) pectic acid, probably a long chain of pyranose-galacturonic acid residues linked in α-glycosidic linkages through the 1, 4 positions, which is found in the middle lamella apparently as a mixture of calcium and magnesium pectates, (2) pectin, a methyl ester of pectic acid, soluble in water and easily hydrolysed to pectic acid by mildly alkaline solutions, and (3) proto-pectin, a substance insoluble in water but soluble in dilute acid, which possibly consists of methyl polygalacturonic chains of greater length than those of pectin These substances, when isolated from the plant and hydrolysed with acid, yield arabinose and galactose, and it was thought that these sugars formed part of the pectin molecule It is now known that these associated sugars arise from the two polysaccharides, araban and galactan, since these polysaccharides can be extracted from the pectic acid by protracted extraction with 70 per cent alcohol

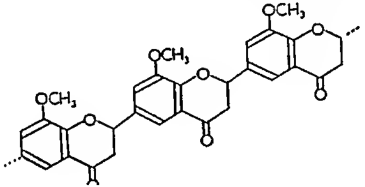
The total pectic substances are usually determined by extraction

with ammonium oxalate solution, hydrolysis of any pectin with dilute alkali and precipitation as calcium pectate. The associated polysaccharides are retained in the precipitate.

An examination of a calcium pectate obtained from cocksfoot (Buston, 1934) showed it to contain about 67 per cent uronic anhydride and 19·5 furfural, and this suggests that the pectate was similar to that found in other plant material. In this particular sample of cocksfoot some 80 per cent of the pectic substances were present as pectate and the remainder as the methyl ester, pectin.

LIGNIN

Lignin is deposited mainly between the microfibrils and micellar strands of cellulose in the secondary cell walls of the plant. The quantity increases as the plant matures and since it is remarkably resistant to degradation by microbiological agencies it provides a barrier preventing the digestion, within the grazing animal, of other plant constituents. Lignin is not a carbohydrate derivative but a high-molecular-weight aromatic complex, the structure of which is not yet completely elucidated although the basic unit is probably a polyflavanone of the type shown below (Ritter *et al.*, 1948).



adopted to reduce the contamination without altering the lignins but none can be considered entirely satisfactory

Moon and Abou-Raya (1954) consider that the lignin of immature pasture plants may be identical with that of mature plants and that although there may be some differences in the methoxyl contents of lignin of different species, the methoxyl content of pure lignin of pasture plants is relatively constant They suggest that true lignin values could be calculated with reasonable accuracy from the methoxyl content of impure lignin preparations

The lignin content of pasture species probably varies from about 2 per cent of herbage dry matter in young herbage to about 12 per cent in herbage at the seeding stage Armstrong *et al* (1950) quote lignin figures for maturing perennial ryegrass, cocksfoot, tall fescue and lucerne, the ranges for the species being 4·7–12·7, 5·5–9·7, 3·8–7·5, and 3·6–7·2 per cent respectively The effect of age on the lignin content of the oat plant has been examined by Phillips *et al* (1939) For three weeks after the date of emergence the lignin content did not exceed 2 per cent At 6, 7, 8 and 9 weeks, the latter being the time of heading the contents were 2·0, 3·2, 4·7 and 6·7 per cent respectively and at 12 weeks the lignin had risen only to 8·4 per cent

THE LIPIDS

The lipids are a complex mixture of fats, waxes, sterols and phospholipids Shorland (1944) examined the lipids of ten samples of cocksfoot collected at different times and obtained the results given below

	Total lipids	Lipids soluble in acetone at 0°C			Waxes	Phospholipids
		Total	Fatty acids	Unsaponifiable		
Mean % on dry matter	6·12	5·06	3·13	0·96	0·86	0·20
Standard deviation	1·05	0·83	0·07	0·17	0·09	0·07

The fatty acids of the true fats varied from 2·15–4·03 per cent of the herbage dry matter The leaf fats differ from the depot fats of animals and seeds in that they contain no oleic acid Over 80 per cent of the fatty acids consists of the unsaturated linoleic and linolenic acids, in

about equal proportions. Palmitic acid is the main saturated acid. Maturation of the herbage causes a decrease in fatty acid content and a reduction in the proportion of unsaturated acids. Also, natural drying, as in haymaking results in a large loss of unsaturated acids (Brouwer and van Albada, 1943).

An examination of saponified waxes of cocksfoot and ryegrass showed they consisted mainly of the long-chain primary alcohol n-hexacosanol (Pollard *et al.*, 1931). Using chromatographic techniques Blair and his colleagues (1953) found the major constituents of lucerne waxes to be C_{29} and C_{31} paraffins and esters, with small quantities of the free alcohols, n-triacosanol and n-octacosanol. On saponification the esters yielded alcohols similar in composition to the free alcohols.

The yield of the labile phospholipids varies with the analytical method adopted. Low yields of 0·1–0·2 per cent obtained on dried cocksfoot and ryegrass can be raised to 1·5–1·7 per cent if the fresh herbage is treated with boiling alcohol (Shorland, 1944). Lecithin, kephalin and a salt of phosphatidic acid are present in the fraction and, in general, the phospholipid fatty acid composition resembles that of the fats of the herbage. The main sterol of herbage plants appears to be sitosterol (Blair, Mitchell and Silker, 1951) and the presence of ergosterol has been noted (Pollard, 1936).

ORGANIC ACIDS

Organic acids are early products of photosynthesis and are intimately concerned in the metabolism of fats, carbohydrates and proteins within the plant. In view of their varying functions a complex mixture of acids would be expected and this is now being demonstrated by developing chromatographic methods. Davis and Hughes (1954) have reported the presence of twelve acids in herbage extracts and have identified acetic, succinic, malic, malonic and citric acids. Hume and Richardson (1954) further identified chlorogenic and quinic acids, and suggest yet another acid is allied constitutionally to quinic acid. Aconitic, tricarballyic and a trace of oxalic acid have been noted in the leaves of cereals by Nelson and his colleagues (1931). De Man and De Heus (1947) also found, by chemical means, appreciable quantities of oxalic acid in perennial ryegrass although none was detected in this grass, cocksfoot and timothy by chromatographic methods (Davies and Hughes, 1954). Quantitatively malic is the most plentiful acid

and together with citric acid constitutes about 50 per cent of the total acids

The total organic acids can represent a very appreciable fraction of herbage dry matter In young perennial ryegrass, cut at various times of the summer, figures of 83 to 144 m equivalent per 100 gm herbage dry matter were obtained (De Man and De Heus 1947) Calculated as malic acid these are 5 6 and 9 6 per cent Ferguson (1948) quotes an equivalent of 11 6 malic acid in young red clover and it seems that clovers generally contain more acids than grasses The limited data available suggest that stage of plant growth and time of year influence the level of acids in pasture grasses, and a diurnal variation is also evident

THE PIGMENTS

The pigments of the chloroplasts of pasture plants are of two groups, the chlorophylls and the carotenoids They are closely associated, which suggests that both groups participate in photosynthesis although satisfactory evidence has not been produced of a part played by the carotenoids

The green chlorophylls, *a* and *b*, are complex esters of the tricarboxylic acid, chlorophyllin ($C_{31}H_{29}N_4Mg\,(COOH)_3$) with methyl alcohol and phytol ($C_{20}H_{39}OH$) The carotenoids, yellow to orange in solution may be divided into two classes according to their composition the hydrocarbons (carotenes) and the far larger class of oxygen-containing pigments the carotenols (xanthophylls) which usually contain at least two hydroxyl groups Practically all carotenoids have 40 carbon atoms

The pigments show an approximate quantitative relationship in green plants and Miller (1938) quotes the following chlorophyll *a* 2 parts, chlorophyll *b* three-fourths of a part, carotene one-sixth of a part and xanthophyll one-third of a part per 1 000 parts green leaf In clonal lines of bromegrass, fully headed and mature, the total chlorophyll ranged from 54 to 211, total carotenoids from 10 2 to 30 3 and carotene from 3 4 to 12 4 parts per million of the dry weight (Johnson and Miller, 1940) In young herbage studied through the grazing season the total chlorophyll content varied from 0 8 to 1 5 per cent of the herbage dry matter and a fairly close relationship existed between chlorophyll and protein contents The ratio chlorophyll *a*/chlorophyll *b* varied from 3 3 to 2 8 (Harberts *et al*, 1954) In white clover the chlorophyll-carotene ratio varied during the year from 18 to 98

and averaged 36, the chlorophyll-xanthophyll ratio averaged 12·5 and the xanthophyll-carotene ratio 2·9 (Beck and Redman, 1940).

Chlorophyll has no apparent direct nutritional value to animals. However, a deep-green leaf colour, indicating high chlorophyll content, is usually associated with high protein and high carotene contents. Xanthophyll likewise has no known nutritional value and carotene is the only pigment of significance in animal nutrition.

The carotene of growing pasture plants is almost entirely β-carotene, the precursor of vitamin A, and the only source of the vitamin for grazing animals. The concentration of carotene is relatively high in young plants and decreases as the plants mature and the proportion of leaf to stem decreases. The carotene content of field-dried hay is usually negligible. Factors ensuring rapid plant growth, such as favourable climatic conditions and an adequate soil supply of nutrients, give rise to high carotene levels in the plants in the early stages of growth. Manuring with nitrogenous fertilizers has a favourable effect on carotene content. Differences between grassland species in carotene content are to be expected since species differ in rate of growth and in their leaf-to-stem proportions. Generally, pasture legumes contain more carotene than grasses and the fall in level with maturity is less marked in the legumes. Very young grasses and clovers can attain carotene contents of about 60 mg. per cent of the dry matter in early spring and in the autumn but this high level is not maintained for long and the values of 20–40 mg. per cent for grasses and 30–50 mg. per cent for legumes represent more general levels in herbage at a normal grazing stage. Carotene, being highly unsaturated, is a very unstable compound and when the plant is cut enzymic, photochemical and oxidative destruction of carotene commences immediately. This fact is of little importance to the grazing animal but is significant in the production of dried grass used as a source of carotene in pig and poultry rations. The losses of carotene, with reasonable wilting and efficient drying, need be only 15–20 per cent but a further 30–40 per cent may be lost during several months of storage (Waite and Sastry, 1949). Low temperatures and exclusion of light and air during storage will minimize the loss.

THE VITAMINS AND SOME OTHER MINOR CONSTITUENTS

Plant material contains no vitamin A and the variations in the level of carotene, the precursor of vitamin A, in grassland herbage have been

discussed earlier Vitamin D seems to be absent in fresh herbage but present in small dead areas of the leaf and in sun-cured hays which have been subjected to ultra-violet radiation Grassland herbage contains a small quantity of ergosterol which is converted to vitamin D by irradiation and the apparent lack of vitamin D in fresh herbage as determined by biological assay may be influenced by the fact that carotene can act as a rachitogenic agent (Grant, 1953, Grant and O'Hara, 1957) Vitamin E is present in grassland herbage but little information is available concerning its seasonal variation Vitamin C, or ascorbic acid appears to be generally present in all green forage, the quantity falling as the plants mature Booth (1942) quotes figures of 40 mg ascorbic acid per 100 gm fresh winter grass and 140 mg for summer grass

Since the components of the vitamin B complex are synthesized in the ruminant animal, the quantities present in grassland herbage have not received much attention The grasses and clovers, however, contain useful quantities of most of these vitamins Thomas and Walker (1949) determined the amounts of B vitamins in a number of grasses and clovers which were at a fairly advanced stage of growth and obtained the following results, the figures quoted being expressed as mg per 100 gm herbage dry matter aneurin 0 2–0 4, riboflavin 0 9–2 0, nicotinic acid 3 3–4 6, pantothenic acid 0 5–1 7, biotin 0 01–0 04 and pyridoxin 0 5–1 4

Glycosides, such as coumarin and related compounds which are haemorrhagic agents, are found in certain herbage species not commonly used in the United Kingdom Commercial white sweet clover (*Melilotus laba*) was reported to contain 0 36 per cent coumarin, 0 27 per cent melilotic acid and 0 05 per cent coumaric acid, and yellow sweet clover (*M officinalis*), 0 65, 0 25 and 0 04 per cent respectively The bitter taste and unpalatability of these species appear to be due to these compounds since *M dentata* which is free of bitter taste contains negligible amounts (Brink and Roberts, 1937)

Saponins are probably present in most pasture plants but only in the legumes is the quantity very appreciable These foaming compounds are of interest in view of their possible role of causal agents of bloat in ruminants (Lindahl *et al*, 1954) The saponins are glycosides, a number of sugars being present in the compounds, and the aglycones, or sapogenins, are of the triterpenoid class In lucerne three saponins have been noted which, on hydrolysis, yielded the sugars arabinose, xylose, glucose and rhamnose, but milder treatment with bromine

water gave rise to spots on paper chromatograms which suggested the presence of three oligosaccharides (Bevenue and Williams, 1955). The sapogenins are very similar to, if not identical with, those found in soya beans (Potter and Kummarov, 1954). Two of the lucerne saponins have been reported as toxic to fish and having the power to haemolyse red blood cells (Walter *et al.*, 1954). Three saponins have also been found in Ladino clover (*Trifolium repens*), the three representing some 0·23 per cent of the clover dry matter (Walter *et al.*, 1955). Hydrolysis gave glucose, galactose, xylose and rhamnose and three sapogenins which were shown to be identical with the soya sapogenols A, B and C of the soya bean. These saponins did not haemolyse red blood cells and were not toxic to fish. No information is available concerning the seasonal variations in the contents of the saponins of lucerne and white clover.

Most plants contain anthocyanin and anthoxanthin pigments which are mainly glycosides but little is known about their occurrence in pasture plants. The anthoxanthins include the widely distributed flavone and flavonol pigments which may occur either in a free form or as glycosides. Interest in such compounds has been stimulated since it has been shown that certain members exhibit oestrogenic properties.

Many of the common species of pasture plants contain oestrogens and in two species of legumes, subterranean clover and red clover, the concentration can be high enough to have pathological effects on the grazing animal. Some lucerne and white clover samples have shown slight oestrogenic activity but many have proved inactive. The legumes generally retain their oestrogenic activity throughout their growth season but the English grasses, ryegrass and cocksfoot, have been found active only during late spring and often not at all during the year. In the Dwalganup variety of subterranean clover, the most potent oestrogenic pasture plant noted, the oestrogen has been identified as genistein, 5:7:4′-trihydroxyisoflavone. Although only a weakly active oestrogen, this substance probably accounts for all the oestrogenic activity of the subterranean clover and can be present, mainly in the leaves, to the extent of 0·75 per cent of the clover dry matter. The oestrogenic activity of red clover, which is lower than that of subterranean clover, is due mainly to its content of biochanin A, 5:7 dihydroxy-4′-methoxyisoflavone, although genistein may make some contribution. The oestrogenic activity of biochanin A is only about 0·6 that of the closely related compound genistein.

In grasses, oestrogenic activity has been found for only about six

weeks in the late spring before flowering and it has not yet been possible to isolate sufficient of the oestrogenic compounds for chemical identification An excellent review by Pope (1954) includes accounts of the physiological and pathological disorders which can be caused by the ingestion of herbage oestrogens the possible influence of these oestrogens on milk quality and the methods adopted for the extraction and assay of the oestrogens

MINERALS

The variability of the mineral content of pasture plants is a very wide subject which cannot be dealt with adequately in this chapter All that can be done is to point out the effect of certain important factors on mineral content and give some indication of the variations which arise under ordinary farming conditions For further information the reader is referred to published reviews by Orr (1928) and by Russell (1944)

The plant depends upon the soil for its supply of minerals and growth can be affected when the soil is deficient in certain elements Absolute deficiency is rare but partial deficiency giving rise to herbage with a low content of a particular element to restriction of growth or perhaps to crop failure is not uncommon In many parts of the world pasture legumes fail owing to lack of molybdenum in the soils and again large areas deficient in phosphorus produce poor yields of herbage containing insufficient of this element to ensure normal bone growth in the grazing animal Soils in many areas are short of certain minor elements not essential for plant growth or needed only in trace amounts e g cobalt and copper but necessary for the well being of the animal Maintenance of a satisfactory level of available elements in the soil is essential therefore for the efficient production of herbage adequate in quality for the grazing animal Another aspect of importance to the grazing animal is the uptake by herbage of elements detrimental to animal health for example the uptake of selenium also molybdenum can reach levels definitely toxic to the grazing animals (see Russell 1944)

Pasture species vary in their ability to utilize soil minerals and this is illustrated by an examination made of four grassland herbs four clovers and eight grasses grown under uniform soil conditions (Thomas *et al*, 1952) The plants were sampled at five stages of growth and the means of the analytical figures obtained are shown in Table 3 8

TABLE 3.8. *Elements in herbs, legumes and grasses*

(% dry matter) (Thomas, *et. al.*, 1952)

	Calcium	Phosphorus	Potassium	Magnesium	Sodium	Chlorine
Herbs	1·41	0·35	3·07	0·75	0·15	0·51
Legumes	1·69	0·38	2·41	0·69	0·07	0·41
Grasses	0·39	0·21	1·99	0·24	0·13	0·50

It will be seen that the herbs and legumes contained considerably more of all the elements quoted, except sodium and chlorine, than the grasses, the most striking difference being in calcium and magnesium contents. Figures for minor elements showed that the herbs and legumes contained more iron and manganese than the grasses but the copper and cobalt contents were rather similar. The related species showed quite wide differences. Within the legume group, lucerne and Alsike showed higher figures than trefoil and sainfoin. In the grasses, meadow fescue, ryegrass, cocksfoot and timothy were generally superior to the other less valuable pasture grasses. The mineral content of herbage varies with stage of plant growth, most elements declining as the plant matures but calcium, and possibly some minor elements, can show very little change. Fagan (1928) working with Italian ryegrass found that over an eight-week period the phosphorus content fell from 0·38 to 0·16 per cent, the potassium from 3·1 to 1·8 per cent whereas the calcium remained fairly constant at about 0·6 per cent.

The highest mineral content which a particular sward can attain will be maintained reasonably well throughout the grass season if the herbage is kept at a young leafy stage by close grazing.

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CHAPTER FOUR

The Nutritional Value of Herbage

D L TRIBE, M FREER AND J B COOMBE

Chemical composition of herbage—Stage of growth—Botanical composition, soil fertility, climate, management—The feeding value of pasture—Digestibility, net energy value, intake, protein value, feeding standards, other factors, seasonal changes

The feeding value of pasture plants has often been described in terms of their gross chemical composition, namely water, crude fibre, crude protein ether extract, nitrogen-free extract and ash In addition to the chemical limitations of this type of analysis, which were outlined in Chapter 3 it must also be remembered that the nutritional significance of the organic constitutents lies largely in the extent to which they contribute to the energy requirements of the animal Therefore it is necessary to take into account their digestibility and the availability of their digested energy for the maintenance of the animal and for productive purposes, as measured by the net energy value of the food

The first part of this chapter deals briefly with the factors which may influence the nutrient composition of herbage and the second part describes the factors which affect the efficiency with which grazing animals utilize these nutrients

THE CHEMICAL COMPOSITION OF HERBAGE

The most important factors which influence the composition of herbage are (1) the stage of growth of the plants, (2) the botanical composition of the sward, (3) the nutrient status of the soil, (4) the climate (5) the management of the sward. Although in practice

these factors are often interrelated it is convenient to consider them under separate headings.

The following sections provide a brief historical review of the development of this field of knowledge. It will be seen that the early work was concerned with the definition of factors which changed the chemical composition of pasture plants, for it was assumed that such changes were necessarily of nutritional significance. Recent work shows a tendency to correlate nutritional value with physiological and morphological changes in plant tissues which may not be reflected in the results of a Henneberg analysis. For this reason the nutritional significance of the results of much of the earlier work is now in question, although the later sections of this chapter make it clear that much more research needs to be done to enable us to predict with confidence the feeding value of a particular association of plants for a particular class of stock.

chemical composition of both Italian ryegrass and red clover varied with the stage of growth during a ten-week growing period. As the plants matured, the proportions of ether extract, crude protein, true protein and ash fell, and the proportions of fibre and nitrogen-free extract rose. (See Table 4.1.)

TABLE 4.1 *Chemical composition of Italian ryegrass at various ages* (Fagan, 1928)

(% dry matter)

	Period of growth in weeks		
	2	6	10
Ether extract	3.8	2.4	2.1
Crude protein	18.8	12.1	6.9
Fibre	20.4	21.6	25.3
N-free extractives	44.4	55.9	60.2
Ash	12.6	8.0	5.5
Calcium (Ca)	0.62	0.65	0.58
Phosphorus (P)	0.38	0.20	0.16
Potassium (K)	3.11	2.63	1.83

Fagan and his colleagues then showed that as a plant matures the proportion of leaf to stem decreases. The leaf at all stages of growth is higher in crude protein, and lower in crude fibre, than the stem at the same stage. Finally as the plant matures the proportion of crude protein falls in both the leaf and the stem, and, conversely, the proportion of crude fibre in leaf and stem rises. More recently Waite and Sastry (1949) confirmed in detail the general principles outlined by previous workers and concluded that the changes which are characteristic of increasing maturity, i.e. a fall in crude protein, ash and ether extract contents, and an increase in the crude fibre and nitrogen-free extract contents, are due partly to the decrease in the leafiness of a sward and partly to the change in composition of both leaf and stem (See Table 4.2.)

Several workers have studied the changes in the ash components of plants that occur as the plant matures. Their results make it clear that the phosphorus, potassium and magnesium contents of the dry matter each fall as grasses and clovers reach maturity. The results are less conclusive concerning the calcium level, but indications are that this does not vary much, or it may even rise, with maturity. These

TABLE 4.2. *Leaf: stem ratio and chemical composition of timothy during growth* (Waite and Sastry, 1949)

(% dry matter)

Sampling date	Ratio leaf: stem	Crude protein L*	Crude protein S*	Ether extract L	Ether extract S	Ash L	Ash S	Fibre L	Fibre S	N-free extractives L	N-free extractives S
May 20	2·57	21·7	14·1	3·8	2·9	7·1	9·9	19·1	23·5	48·3	49·6
June 2	1·30	17·2	11·4	4·7	2·5	6·5	7·9	23·8	29·7	47·8	48·5
June 16	0·39	18·5	7·6	4·1	2·6	8·0	6·6	26·1	32·6	43·3	50·6
June 30	0·35	12·3	4·4	3·3	1·7	8·8	5·0	26·9	31·7	48·7	57·2
July 14	0·20	11·1	3·4	3·2	1·3	9·0	5·0	30·6	32·4	46·1	57·9

* L = leaf, S = stem

changes were again illustrated by the work of Fagan and his colleagues, who showed that the grass leaf is richer in both calcium and nitrogen than the stem, but the phosphorus contents are similar. As the plant matures the phosphorus and nitrogen contents of the leaf gradually fall, but the calcium content increases, whilst in the stem the nitrogen, phosphorus and calcium contents all decrease.

Little work has been done on pasture as a source of water-soluble vitamins because it has been thought that the bacteria in the rumen could synthesize all the requirements of the host animals. Thomas and Walker (1949) analysed various pasture species, cut at the hay stage, and concluded that such herbage is not a good source of members of the vitamin B complex. However, the results of Phillipson and Reid 1957) and Buziassy and Tribe (1960*b*) indicate that the levels of thiamine, riboflavin and nicotinic acid in herbage at a younger stage of maturity are all high. The work of Buziassy and Tribe (1960*a*) also supports the growing opinion that, when fed rations, such as normal herbage, which contain fairly high levels of the B-vitamins, the levels of vitamin synthesis in the rumen are low.

Although it is thought that most grazing animals do not require a dietary supply of vitamin C (ascorbic acid), pasture plants are regarded as a good source of it. However, the vitamin C potency of a plant decreases as the plant matures.

Several workers (e.g. Davies *et al.*, 1953; Waite and Sastry, 1949) have shown that as the plant matures its content of carotene (the precursor of vitamin A) decreases, and a highly significant positive

correlation has been reported between the protein and carotene contents of herbage It is only under extreme pasture conditions, such as drought conditions in Australia that the carotene intakes of grazing stock are likely to fall low enough to result in clinical signs of avitaminosis

Pastures contain ergosterol (the precursor of vitamin D) but there is little information on the adequacy of this source According to Blaxter (1952) the small dead areas of leaves are richest in vitamin D and therefore, because of the irradiation effects mature pasture is a better source of this vitamin than is young herbage

Herbage is generally regarded as a good source of vitamin E

THE BOTANICAL COMPOSITION OF A SWARD

Although as Wilson pointed out the differences in chemical composition between grasses at the same stage of maturity are small compared with differences at various stages of growth, nevertheless these differences do exist, and therefore the nutritive value of a sward will be influenced by its botanical composition The species of a pasture mixture may be divided into three groups grasses, legumes and herbs Shapter (1935) working in South Australia, analysed various members of these three groups and found that the mean protein content for 4 legumes was 21 8 per cent for 11 grasses it was 7 4 per cent, and for 5 herbs it was 12 per cent These findings support those of Fagan (1928) who compared red clover with Italian ryegrass In addition Snider (1946) and workers in New Zealand (Walker *et al*, 1954) have found that grasses grown with legumes have a higher crude protein content than grasses grown alone Workers at Aberystwyth (Davies *et al* 1953, Davies and Davies 1956) found that the presence of legumes in the sward not only increased the percentage of crude protein in the dry matter of the herbage and the total yield of crude protein, but also increased the carotene content of the herbage

As well as detecting differences in protein content between his three groups Shapter (1935) also found significant differences in mineral content The average value for soluble ash in herbs was high, 12 5 per cent, for grasses it was lower, 6 6 per cent, and for legumes it was intermediate, 9 2 per cent A number of experiments has been done to compare the calcium and phosphorus contents of legumes and grasses and in general the results show that legumes are richer in total ash and calcium than grasses, although grasses are richer in phosphorus (e g Fagan, 1928, Ripley *et al*, 1949, Snider, 1946) Davies *et al*,

(1953) found that legume–grass associations were richer in total ash and calcium, and poorer in phosphorus than grasses alone. Svanberg (1949) has shown that legumes are richer in magnesium than are grasses. The effect of introducing legumes, therefore, is to increase the percentage of crude protein, total ash and calcium and magnesium of the herbage.

An interesting point from Shapter's figures quoted above is the high mineral content of herbs, many of which are classed as weeds. Some groups of workers have considered the advisability of deliberately introducing these into pastures to raise the mineral content of the herbage. That pasturage may supply insufficient amounts of minerals to the grazing animal under certain circumstances has been argued by Blaxter (1952) and in many parts of the world it has been shown that pastures may not support full productivity of animals because of mineral deficiencies.

Thomas *et al.* (1956*a*, *b*) compared four different swards containing 22 per cent, 14 per cent, 7 per cent and 0 per cent herbs. They showed that total yields of dry matter were decreased by an increasing percentage of herbs, and that other undesirable effects were a decrease in the contents of digestible crude protein and total sugars, and an increase in the crude fibre and lignin contents. However, inclusion of herbs increased the percentages of all the ash constituents except sodium, potassium, copper and cobalt. In a further experiment, where the pasture was cut for hay, the same results were obtained. These workers came to the conclusion that a cover of more than 15 per cent herbs was undesirable.

Tribe, Gordon and Gimingham (1952) reported an experiment in which one group of young dairy heifers grazed a grass and clover sward and a second group grazed a similar sward plus an area of herbs. There was no difference in the productivity or grazing behaviour of the two groups, but the inclusion of the herbs resulted in a reduction in the production of digestible nutrients per acre.

As well as differences in composition between the three main groups of herbage plants, there are differences between species within these groups, and also differences between different strains of one species. For example, Mitchell (1954) showed that species of herbs differed markedly in their capacity to absorb trace elements from the soil. Working with legumes, Snider (1946) showed that red clover was lower in crude protein and total ash contents than was lucerne, and this was confirmed by Ripley *et al.* (1949) who also reported small differences

between white clover and lucerne Some work with grasses was also reported from Illinois where Snider showed that Kentucky blue grass and brome grass had higher contents of protein and minerals than other grasses Phillips *et al* (1954) confirmed this nutritional superiority of Kentucky blue grass and also showed that *Phalaris* was comparatively rich in protein Fagan and Milton (1931) observed that different grass species showed variations in their mineral contents, even though at the same stage of maturity, and Bosch (1954) noted the high content of potassium in cocksfoot, and the high sodium content of perennial ryegrass

The differences in chemical composition between different strains of a species are usually smaller than those between different species, however, they do occur, and they are often related to the leafiness of the strain At the Welsh Plant Breeding Station (Fagan, 1929), indigenous strains of cocksfoot and timothy produced a pasture higher in protein than commercial strains of the same grasses, simply because they had a higher leaf stem ratio

FERTILITY OF THE SOIL

The third factor affecting the nutritive value of a pasture sward is the ability of the soil to supply the plant with nutrients, and this, of course, is intimately bound up with the fertilizer treatment

The level of a mineral in a plant depends partly on the availability of that mineral in the soil This effect is superimposed on the effects of stage of growth and the species of plant concerned For example Richardson *et al* (1931) reported an experiment done in Australia in which Italian ryegrass was grown on three different soils Analyses of soil and plant were made for soluble ash, calcium, phosphorus, nitrogen and potassium, and it was shown that the levels of these nutrients in the plant were proportional to the levels in the soil In the case of many elements, e g nitrogen, calcium, phosphorus, potassium, magnesium, sulphur and copper, a low level in the soil is often reflected in a decreased productivity of the sward or of certain of its constituents, particularly legumes Additions of fertilizers are therefore primarily used in order to satisfy the nutritional requirements of the plant, rather than to alter the plant's composition in order to improve the nutrition of the grazing animal However, a deficiency of cobalt in the soil apparently does not normally affect plant growth and therefore when cobalt fertilizers are used the purpose is to alter the chemical composition of the herbage, rather than its productivity

or health. A recent paper (Ahmed and Evans, 1959) has indicated, however, that cobalt is probably necessary for the adequate fixation of nitrogen by leguminous plants.

The application of fertilizers may affect the feeding value of herbage in several ways. Fertilizer treatment may remedy the deficiency of a particular nutrient in the soil, and hence a deficiency of this nutrient in the herbage. In so doing it will change a vegetation of negligible food value into a pasture of high nutritional value. Examples of this effect are the applications of copper, cobalt and zinc to extensive areas in Australia where neither intensive plant nor animal production was previously possible, and the application of phosphatic fertilizers to deficient soils in South Africa. The second, and more general, way in which a fertilizer may act, is to increase the content of the appropriate element in the dry matter of the herbage. In the majority of cases, although no clinical deficiency is remedied in either plant or animal, the feeding value of the herbage is improved. Almost all fertilizers have been shown to produce this effect; thus the application of the appropriate fertilizers has been shown to increase the contents in the plant of calcium and phosphorus (Fagan, 1928), potassium (Bosch, 1954), magnesium (Stewart and Reith, 1956), and sulphur (Hilder and Spencer, 1954). In addition to these direct effects there may be interaction in the soil between some of the minerals. For example, the application of lime to the soil can cause effects other than an increase in the calcium content of the herbage; for example, it will increase the availability of molybdenum and thus result in a subsequent rise in the legume content of the pasture. However, liming can also depress the availability of manganese, zinc and iron in the soil, with a subsequent lowering in the concentrations of these elements in the plants.

Another way in which fertilizers may affect the feeding value of herbage is by altering the botanical composition of the sward. In Australia, Hilder and Spencer (1954) found that fertilization with sulphur increased the proportion of legumes in the sward, with a subsequent increase in the crude protein content of the herbage. Similarly a well-known effect of phosphatic fertilizers is to encourage the development of clovers in the sward, particularly when the soil is moderately deficient in phosphorus, as in the continents of Africa and Australasia.

The application of nitrogenous fertilizers merits special mention, because these are used extensively on grasslands in some countries. Such fertilizers, when applied to grasses, increase their nitrogen contents.

Mulder (1949) showed that an application of 0 4 cwt nitrogen per acre increased the crude protein content of the dry matter of young grass from 16 6 per cent to 28 per cent He also showed that an increase in the true protein content paralleled the crude protein figures However, when nitrogenous fertilizers are applied to pure legume swards the percentage of nitrogen in the dry matter of the legumes is only increased when the dose rate is exceptionally high If nitrogenous fertilizers are applied to legume–grass associations the percentage of legumes is often depressed, and the percentage of grasses is correspondingly increased. At levels of 0 6 cwt nitrogen per acre Walker *et al* (1953) found this depression of legumes to be 20 per cent Thus nitrogenous fertilizers produce opposing effects an increase in the crude protein content of the herbage particularly with grasses and a decrease in the crude protein content due to suppression of legumes

The ultimate effect of a nitrogenous fertilizer on the crude protein yield of a legume grass mixture will depend on three factors (*a*) the change in yield of dry matter (*b*) the increase in the crude protein content of the grasses (*c*) the decrease in crude protein yield due to decrease of clovers In an experiment carried out in New Zealand, Walker *et al* (1953) compared three markedly different rates of nitrogen application on a ryegrass/white clover sward, and found that the total yield of nitrogen from the crop was practically the same for all three treatments In an experiment in England (Walker *et al* 1952) it was shown that on predominantly grass plots applications of a nitrogenous fertilizer increased the yield of dry matter and the yield of crude protein

It was once thought that the increased percentage of nitrogen in the dry matter of fertilized herbage might to due to a large increase in non protein nitrogen levels However Mulder (1949) showed that the crude protein content also reflected the true content and work by Ferguson and Terry (1956) indicated that non protein nitrogen levels were not raised markedly by fertilization with nitrogenous compounds

Fagan (1928) reported experiments on the effect of farmyard manure and liquid manure applied to pasture to be cut for hay Heavy dressings of farmyard manure had a negligible effect on the mineral composition of the dry matter but caused a slight decrease in the fibre content and an increase in the crude protein content Liquid manure had a similar effect on fibre and crude protein levels and also slightly increased the content of soluble ash calcium potassium and chlorine

In general Fagan concluded that these manures had only a small effect on the chemical composition of the sward, but were important in increasing the yield.

CLIMATE

The climate of a region exerts its effect by determining the species of plants that will grow in the area. The most important aspect of the climate is the length of the growing season, i.e. the period when moisture and temperature conditions are suitable for active plant gowth. The longer this period is, the better will be the overall nutritive value of the herbage, because the pasture will contain those species which have a long growing period. These species remain at the immature leafy stage of growth for a long time, and, as has already been discussed, this stage gives herbage of the highest feeding value. It is a general case that the longer the life cycle of a strain or species of plant, the leafier it is. Thus the inclusion of later strains means a leafier pasture, with a consequent improvement in nutritive value. Thus the climate is important because it determines the botanical composition of the sward.

In addition, the climate affects the supply of nutrients from the soil. A high rainfall generally causes the soil to be poor in nutrients because of extensive leaching of soluble nutrients from the upper horizons.

Donald (1941) claims that climate can be a cause of poor chemical composition apart from any variations of soil, species or stage of growth. He drew attention to the low nutrient content of pastures in tropical and sub-tropical areas compared with those of temperate regions and states that the climate is directly responsible for this. Thus, in tropical regions, the high temperature during the rainfall season enable very active photosynthesis to proceed, resulting in a greater relative dilution of nitrogen and minerals available from the soil, and, consequently, in herbage very low in crude protein and ash contents.

Seasonal climatic conditions generally affect the total yield of herbage more than they affect its chemical composition, although in certain circumstances they may affect both.

Seasonal conditions can also affect the availability of nutrients from the soil. Ferguson (1931) reported that the herbage contents of soluble ash, nitrogen, phosphorus, potassium and, to a lesser extent, sodium, were decreased by dry conditions, and increased with rainfall. Greenhill and Page (1931) also found that the phosphorus contents of herbage fell during droughts, and advocated that fertilizers richer in phosphorus

than in calcium should be applied during dry conditions These findings were confirmed in general by later work in Germany Summing up these findings, it appears that moist conditions increase the proportions of nitrogen phosphorus and potassium in herbage During dry conditions the nitrogen and phosphorus levels in particular will be depressed, potassium levels will be depressed to a lesser extent, and calcium levels will be maintained.

Seasonal conditions may affect the botanical composition of the sward, and in this way alter the chemical composition of the herbage For example, Roseveare (1947) showed that *Phalaris* was more resistant to prolonged spring flooding than timothy Similarly Davis and Martin (1949) found that ryegrass, cocksfoot and white clover were killed out readily by being submerged, whereas several grasses, e g meadow foxtail and *Agropyron*, were resistant to flooding It is also well recognized that particular species or strains are better adapted than others to such factors as high or low temperatures, drought, and day-length, and indirectly such influences on pasture composition will also affect the feeding value of the sward

THE EFFECT OF MANAGEMENT

In general the basic object of pasture management, from the point of view of the grazing animal, is to arrest the normal pattern of herbage development, as far as climatic conditions permit, and to maintain the sward in a leafy condition for as much of the season as possible

Some control can be exercised by selection of pasture species with a long vegetative stage and by the use of special leafy strains within these species To some extent the period of leafy growth can be spread by the use of a series of special-purpose pasture mixtures with characteristics of early or late growth. Again fertilizers, particularly nitrogen, can be used to extend the period of leafy growth, increase the leaf stem ratio and raise the protein content of the leaf, while phosphatic and sometimes potassium fertilizer increase the clover component of the sward and with it the overall quality of the food.

It is through grazing management, however, that the greatest degree of control can be exerted over pasture quality The fine balance existing between the plant community and the grazing animal in the maintenance of the sward was illustrated by Jones's (1933) work on the effect of the seasonal distribution of grazing pressure on botanical composition. Different herbage species could be suppressed or encouraged by very heavy or light grazing respectively at the time at

which they were making vigorous growth. In this way the balance of grasses and clovers, leafy grasses and weeds could be altered or maintained. Maintenance of a well-balanced sward was achieved in Jones's experiments by a system of rotational grazing with grazing pressure distributed over the season in proportion to the available herbage.

The grazing animal arrests the normal maturation process of the plant by defoliation at intervals during the season, and the plant responds by producing fresh leaf material of high nutritive value. In investigations of the effects of frequent defoliation on the yield of herbage nutrients many workers have used cutting techniques to simulate grazing. Under these conditions, frequent defoliation during the vegetative stage, before the growth has reached its maximum level, has usually been found to reduce the total seasonal yield of herbage. However, the translation of the results of such experiments to grazing conditions is complicated by the more gradual defoliation of the plant by the animal and by its return of nutrients to the sward, tending to moderate the effects of frequent defoliation. In practice, nutrient yield is more likely to be depressed by too low a frequency of defoliation, and when environmental conditions favour rapid herbage growth, or when the herbage plants have a short period of vegetative growth, it may in fact be found that continuous grazing is a more suitable technique than rotational grazing for maintaining the nutritive value of the sward.

It is clear that nutritive value cannot be considered in isolation from total herbage yield. The two factors are mutually opposed and the conflict constitutes a problem in grazing management that can be resolved only in relation to all the other aspects of the grazing complex, such as intensity of stocking and selective grazing habits. In practice, however, it is rarely possible to adjust stocking rates to cope with seasonal differences in pasture growth rate and an overall stocking rate is fixed to achieve the best compromise over the season.

In the final analysis the system of management can be judged only by the yield of animal production per acre, and maximum production per acre can be obtained only from a system which ensures complete utilization of available pasture at every grazing. The only practical way of reducing selectivity of grazing to this point is to raise the stocking rate so high that production per animal is depressed. Under these conditions the food available may be higher in protein and lower in fibre than necessary, or perhaps even desirable, from a purely

nutritional viewpoint, but this condition is inseparable from the system of management

It must be remarked, however, that this argument applies to the technical question of efficient pasture utilization, and may not apply to the economic considerations associated with certain forms of livestock production

THE FEEDING VALUE OF PASTURE

Within limitations set by the climate and the fertility of the soil, the chemical composition of herbage will be determined primarily by its stage of growth, through the direct effect of this on the development of the structural and floral components of the plant and also on the distribution of tissue between leaf and stem If undisturbed by defoliation, this process results in a seasonal pattern of change from a food high in soluble carbohydrate and protein and low in crude fibre, able to sustain high levels of milk production, to a fibrous material often incapable of maintaining a dry cow

These changes in the feeding value of herbage are a reflection of the effect of the changes in its composition on the amount of energy which the animal can retain from its daily intake of the herbage This will be determined firstly by the amount of herbage eaten and secondly by the proportion of the food energy which remains after the loss of energy in the faeces, in rumen fermentation and in urine excretion

As differences between herbages in their content of net energy are due mainly to variable faecal losses, the simplest and at the present time the most useful measure of herbage feeding value is its digestibility Direct estimations of net energy values are rarely carried out and the results are as yet too limited in their application to be of practical use in evaluating herbage Indirect estimation by the conversion of digestibility data, although commonly practised in the starch equivalent system, is accompanied by large errors due to the arbitrary correction factors used

DIGESTIBILITY OF HERBAGE

In general an advance in the stage of growth of a pasture plant is accompanied by a decrease in its digestibility It appears that this is due to the progressive organization of cell wall material at the expense of soluble cell constituents and the gradual encrusting of the cellulose by lignin which protects it from the action of the ruminal flora The

association between this decline in digestibility and the changing pattern of chemical composition has been investigated by many workers with the aim of establishing accurate relationships which would enable the digestibility to be predicted from the chemical analysis without recourse to digestibility trials.

Examination of the results of numerous digestibility determinations on fresh and conserved herbage has shown that there is a high negative correlation between the content of crude fibre and lignin and the digestibility of the herbage organic matter (Lancaster, 1943; Forbes and Garrigus, 1950; Walker and Hepburn, 1956). So long as the application of regression equations based on such correlations is restricted to the types of herbage from which each equation was derived, they may give some measure of large differences in feeding value. However, the errors of prediction associated with the regression equations so far obtained are still too high for the method to be of practical use in the evaluation of herbage (Raymond *et al.*, 1960). Although refinements of analytical technique to isolate more precise chemical constituents may increase the accuracy of this approach it is now becoming clear that the changes in digestibility which occur during the growth of a grass are intimately related to the degree of organization of its cellular material and that this may be poorly reflected in the results of chemical analysis.

Recent work suggests that a more precise index of the digestibility of the first growth of a grass is the time interval between the date on which ear emergence begins and the date of cutting; and for regrowths, the time interval between successive defoliations. Minson *et al.* (1960) showed that the organic-matter digestibility of the first growth of a grass remained fairly constant until the beginning of ear emergence, despite a decline in leaf lamina percentage and crude protein content. Following ear emergence the digestibility coefficient declined at a rate of approximately 0·5 units per day. Differences between strains of ryegrass (S23 and S24) were wholly related to differences in the date of ear emergence but there were specific differences between grasses. The digestibility coefficient of S37 cocksfoot was always lower than that of ryegrass cut at the same stage of growth and the average difference was 5·5 units. The difference was maintained in regrowths cut at monthly and two-monthly intervals. As the season advanced there was a gradual decline in the digestibility of the regrowth cuts from all grasses, despite an increase in the leaf lamina percentage.

The rapid fall in digestibility after ear emergence is accompanied by

a similar change in the concentration of water-soluble carbohydrates and Tilley *et al.* (1960) have suggested that this is due to the progressive increase in the proportion of indigestible cell wall material, at the expense of those plant constituents which are dissolved or suspended within the aqueous part of the plant.

Although these methods of evaluating herbage have an immediate application in the timing of a conservation programme for the maximum yield of digestible nutrients, their use under grazing conditions is limited by the degree of selection exercised by the animal. This will vary according to the intensity of stocking but Hardison *et al.* (1954) found in one experiment that, even under fairly intensive management, grazed samples of herbage were 6 per cent more digestible than clipped samples.

To avoid the errors associated with attempts to sample herbage 'as grazed' direct relationships have been sought between the digestibility of the herbage eaten and the chemical composition of the faeces. Of the two faecal constituents most successfully used as indicators nitrogen was first suggested by Lancaster (1949) and, due mainly to the relative simplicity of its analysis, it has been generally preferred to 'chromogen' (plant pigments and their breakdown products extracted by 85 per cent acetone) the indicator proposed by Reid *et al.* (1952).

The relationship between faecal nitrogen and herbage digestibility rests on the preponderance of the metabolic fraction in the faecal nitrogen of ruminants. Over a wide range of nitrogen intake the output of faecal nitrogen is almost entirely dependent on the weight of dry matter eaten and to only a small extent on the nitrogen content of the herbage (Hutchinson, 1958). It follows that the nitrogen content of the faeces must be closely related to the digestibility of the herbage. However, unacceptably large errors of prediction are associated with regression equations derived from a range of herbage digestibility data and although these may be reduced by the use of 'local' regression equations restricted to a particular type of herbage (Raymond *et al.*, 1956), Minson and Raymond (1958) have shown that the errors are very largely due to differences in the date of cutting of the herbage from which the equation is derived. They concluded that for critical comparisons of digestibility, the regression equation should be derived from herbage cut, during grazing, from the sward to which the equation is to be applied. Although, in addition, the prediction may be biased by differences in the level of intake and the degree of helminthiasis between the grazing animals and those used for digestibility

determinations, the faecal index technique provides, at present, the most satisfactory approach to the evaluation of grazed herbage.

NET ENERGY VALUE OF HERBAGE

The value of digested energy to the ruminant depends on the amount of energy lost in rumen fermentation and urine excretion, and on the efficiency with which the remaining metabolizable energy can be used by the animal. The main source of this energy (Phillipson, 1959) is provided by the volatile fatty acids which are produced in the rumen from the anaerobic fermentation of carbohydrates and from the deamination of amino acids. Therefore the net energy value of the food will be determined largely by the amounts of the different acids produced and the relative efficiency with which they can be used for maintaining the animal and for productive purposes.

Acetic, propionic and butyric acids make up more than 90 per cent of the total acids found in the rumen but their relative proportions may vary considerably. Tilley *et al.* (1960) analysed the rumen liquor of sheep fed a wide range of herbages and found that the ratio of acetic acid to propionic acid varied from 3·1:1 to 1·7:1. Similar differences were found in the proportion of volatile fatty acids produced by the *in vitro* fermentation of these herbages. Herbage with the high content of soluble carbohydrates associated with an early stage of growth tended to produce the highest proportion of propionic acid. However, these differences will not affect the ability of the herbage to maintain the animal, as widely different mixtures of these acids can be utilized with equal efficiency for this purpose (Armstrong *et al.*, 1957). In other words the nutritive value of a herbage for maintenance depends almost solely on its content of digested energy.

When the level of intake is higher than that required for maintenance the metabolizable energy from the food is used less efficiently and it now appears that the extent of this depression depends on the type of rumen fermentation promoted by the food and the consequent proportions of the different fatty acids which are metabolized. Although the quantitative aspects of energy retention in terms of volatile fatty acid utilization are not yet clear, it is apparent that there are differences between the acids in their increments of heat loss (Armstrong *et al.*, 1958) and that these differences may vary with the type of tissue or animal product being synthesized. The possibility that individual fatty acids absorbed from the rumen may also have specific roles in

metabolism has been demonstrated with respect to the synthesis of milk constituents by Rook and Balch (1959*a*)

Although the digested energy of a herbage may therefore be a less precise index of its net energy value for production than of its value for maintenance, it appears that in general digestibility is closely related to the availability of the digested energy for production For example Armstrong (1960) found that while an early cut sample of ryegrass was 41 per cent superior to a late cut in supplying net energy for maintenance, due almost entirely to the difference in digestibility, it was 83 per cent superior in supplying net energy for fattening

Although current research aimed at establishing the efficiency of the various metabolic pathways followed by the products of rumen fermentation should eventually enable herbages to be evaluated in terms of the particular needs of the animal, at present it is usual in European countries to estimate the net energy content of a herbage, as with other foods in terms of its starch equivalent The starch equivalent of a food is normally determined by indirect estimation from digestibility data Standard conversion factors are used to account for the loss of digested energy in rumen fermentation and urine excretion and an arbitrary correction, based on the crude fibre content of the food, is made for the lower availability of the metabolizable energy from less digestible foods However no account is taken of the effect of the level of feeding on the net energy value

THE INTAKE OF HERBAGE BY THE GRAZING ANIMAL

The other main factor determining the intake of net energy from a herbage is the appetite of the animal It appears that the voluntary intake of a roughage by a ruminant is regulated in relation to the load of food residues in the alimentary tract (Blaxter *et al*, 1956) the daily intake varying with the rate at which this load diminishes through digestion and the passage of digesta through the tract There is therefore a close relationship between the quality of a herbage, as measured by its content of digested energy per unit weight, and the amount which the animal will eat (Crampton 1957) It follows that a small increase in the digestibility of a herbage can have a relatively large effect on the intake of digested energy and particularly on the amount of energy available for productive purposes This is well shown in Table 4 3, taken from Blaxter (1960) A difference of 30 units of digestibility between two roughages led to a twelve-fold difference in the amount of digested energy available for productive purposes

TABLE 4.3. *The food intake of sheep fed ad lib., and their resultant gains, expressed per unit of metabolic body size (kg $W^{0.73}$)*

From Blaxter (1960)

Food	Apparent digestibility of energy %	Appetite g dry matter	Digested energy kcal	Energy digested in excess of estimated maintenance requirement kcal	Observed gain/day g
Poor hay	44	58	117	16	+0·7
Medium dried grass	60	82	223	123	+5·4
Good dried grass	74	94	317	216	+9·4
% Difference $\frac{(\text{Good}-\text{Poor})}{\text{Poor}} \times 100$	+69	+62	+171	+1250	+1240

In areas of the world where poor-quality roughages provide the main source of energy for ruminants, ways of improving their appetite for this material have recently been investigated. Since the rate of rumen digestion will largely depend on the level of activity of the ruminal flora, it follows that any dietary factor which will increase microbial rates of metabolism may also result in an increased appetite of the host animal. Moir and Williams (1950) have shown that the intake of nitrogen is an important factor determining the rate of proliferation of the rumen bacteria and it has been found that the addition of nitrogen, as urea, to rations of low-quality herbage markedly improves roughage intake by sheep (Williams *et al.*, 1959) and cattle (Morris, 1958).

On the other hand, with lush young herbage it is frequently claimed that the moisture content, which is often as high as 84 per cent, may limit the dry matter intake by increasing the bulk of the ration. However, there is little experimental evidence for a decrease in the appetite of grazing animals with access to an adequate quantity of this type of herbage.

Since the composition of the diet of the grazing animal is dependent on a process of free selection, food preferences shown by the animal are of interest in relation to its intake of nutrients. The palatability of a herbage is a function of the animal rather than the plant (Tribe, 1952) but changes within the plant can modify this to a considerable extent. Its stage of maturity is known to be an important factor (Davies, 1925)

and most of the observed differences in acceptability of pasture species and strains can be attributed to their stage of growth at the time Differences in acceptability may therefore have a significant effect on the nutrient intake of animals on pastures containing plant material at widely different stages of maturity

On the other hand, the nutritional significance of the selection preferences shown in a particular field of young herbage is doubtful. Although under conditions of restricted grazing the cattle studied by Hardison *et al* (1954) selected a diet 6 per cent more digestible than the total available herbage, these workers emphasized that this does not indicate active selection of nutrients by the animal but is rather a consequence of the physical characteristics of the leaves and their relative accessibility to the animal Under these conditions acceptability is only a relative term depending on the intensity of grazing management The apparent acceptability of herbage increases as the stocking rate is raised and the opportunities for selective grazing are reduced to a minimum Whilst an animal that is allowed full scope for selective grazing would obtain a higher intake of digested energy than one grazed intensively, this would be at the expense of efficient pasture utilization which is essential for maximum animal production per acre of pasture

Any consideration of the factors affecting the energy intake of grazing animals has always been severely handicapped by the difficulty of measuring it with sufficient accuracy However, the technique which depends on the mathematical relationship of the intake of food to its digestibility and the output of faeces as estimated from the concentration of indicator substances in the faeces has been markedly improved in recent years by reducing the errors associated with these estimations (Minson and Raymond, 1958, Corbett, 1960)

THE PROTEIN VALUE OF HERBAGE

The value of a protein to a ruminant is determined, first, by the extent of deamination in the rumen and the degree to which the non-protein nitrogen released there can be used for the synthesis of microbial protein, and second, by the fate of dietary protein which reaches the duodenum unchanged. However, the quantitative aspects of these processes are as yet unknown Although the ingestion of young pasture is generally followed by a particularly high concentration of ammonia in the rumen liquor (Johns, 1955) due to the ready solubility of the protein, the feeding value of such herbage is never limited by

its protein content. At the other extreme, in roughages prepared from herbage cut at an advanced stage of maturity, the protein content may be inadequate to maintain the animal in positive nitrogen balance, through the combined effect on the intake of energy and of digestible protein. Although the true digestibility of protein in herbage is high and does not appear to be much affected by the protein content of the food, the apparent digestibility, which is of more concern in the nitrogen economy of the animal, is very highly correlated with the protein content. It appears that this is due to the increase in the output of metabolic faecal nitrogen as the protein content declines and as the crude fibre content of the food increases (Reid *et al.*, 1959).

In the absence of an appropriate measure of protein value for ruminants, the feeding standards are based on the protein equivalent of the food. This is the content of digestible true protein with an increment equal to half the content of non-protein nitrogen. This standard was adopted because of the variable economy of utilization of non-protein nitrogen by the rumen bacteria.

FEEDING STANDARDS FOR GRAZING ANIMALS

The starch equivalent system of feeding standards was designed for the guidance of farmers in rationing stall-fed animals, and it attempts to equate the intake of net energy by the animal with its net energy requirements. Woodman (1948) has published tables showing average values of these standards for various classes of stock. The requirements for maintenance are calculated in relation to the size of the animal (in theory to its metabolic size, or two-thirds power of the body weight) with, in the case of grazing animals, an increment for the additional energy expended. The results of calorimetric experiments (Blaxter, 1960) suggest that this increment is unlikely to raise maintenance requirements by more than 10 per cent. The doubtful validity of the use of starch equivalent system for assessing energy requirements for productive purposes and for evaluating the food sources of this energy, has already been discussed. When the feeding standards are used for meat-producing animals at grass these errors are aggravated by the difficulty of measuring and interpreting body weight changes. For these reasons, and also because the farmer is usually unable to measure the amount of herbage eaten, the system is of limited practical use for grazing animals. It is probably true to say that under these circumstances the system is used more often in reverse for estimating the energy intake of groups of animals or the yield of utilized

energy from pastures than for predicting animal production from herbage

However, a consideration of the effect of pasture quality on the level of animal production does show the very high feeding value of frequently grazed herbage The high digestibility and high voluntary intake of this material combine to provide a cow with sufficient energy and more than enough protein for the daily production of 50–60 lb of milk. As the digestibility of the herbage falls, due to an increased interval between grazings, milk production is limited at first by the lower intake and lower availability of the digested energy, and later by the content of digestible protein which falls at a relatively faster rate than the content of net energy Although this suggests that increased production might be obtained by the use of energy-rich supplements on the highest quality pasture and by protein-rich supplements on poorer herbage the results of several experiments reviewed by Holmes and Sykes (1960) show that where an adequate supply of good herbage is available for milking cows, supplementation with concentrate food is rarely worth while The average response in these experiments to 1 lb of supplementary food was only 0 3 lb of milk, largely due to a complementary reduction in the amount of grass eaten by the supplemented cows

OTHER FACTORS AFFECTING THE NUTRITIVE VALUE OF VERY YOUNG HERBAGE

With very young herbage there is some evidence that the emphasis which has repeatedly been placed on the relationship between stage of growth and feeding value, requires some qualification This herbage has a high content of water, crude protein and soluble carbohydrates and a low content of crude fibre Although some of the effects of these factors on ruminant digestion will be mentioned, it is probable that some of the criticisms levelled at the feeding value and acceptability of young spring pasture arise because of an inadequate supply of herbage at the time when the animals are first turned out to grass Animals on spring herbage appear to scour and hay is frequently offered to prevent the 'ill effects' of this condition However, Rook and Balch (1959*b*) have shown that the fluid consistency of the faeces at this time may be due simply to the effect of the high digestibility of the herbage and its low content of structural components on the output and texture of the faecal dry matter, and does not involve the excretion of an increased amount of water and minerals in the faeces

An abnormal depression of the butterfat percentage in the milk of cows grazing very young grass has occasionally been reported and McClymont (1950) was able to produce a 40 per cent depression on short pasture supplemented with concentrates. The depression could be prevented or corrected by feeding coarse roughage. This condition is similar to the one produced by Balch *et al.* (1955) in cows fed rations containing a high ratio of concentrates to roughage, particularly when the hay was ground and the concentrates were rich in starch. On these rations, as on young herbage (Tilley *et al.*, 1960), the rumen liquor contains a relatively high proportion of propionic to acetic acid and it appears that this results from the effect of the high level of soluble carbohydrate and low content of fibrous material on the type of rumen fermentation. Recent work by Rook and Balch (1959*a*) suggests that the effect of these rations on milk composition is due to specific and opposite effects of acetic and propionic acids on the synthesis of milk fat; dietary factors that cause an increase in the relative proportion of propionic acid produced in the rumen may lead to a depression in the milk fat percentage. The indication from this work that propionic acid has also a specific and positive effect on the synthesis of the solids-not-fat fraction of milk, may help to explain the marked increase which frequently occurs in the solids-not-fat content of milk from cows after changing to spring pasture.

The high content of crude protein in young grass frequently contains a high proportion of non-protein nitrogen compounds, and in particular, of inorganic nitrate. Butler (1959) has studied the chemical composition of rapidly growing ryegrass and its relation to animal production, and has defined factors which influence the nitrate content of herbage. Althougb, under field conditions, particularly in the autumn, the nitrate content is known to reach levels which are potentially toxic to stock, it is at present believed that the general unthriftiness which has been reported of stock grazing this herbage is more likely to be due to other constituents of the plants, or to a combination of high nitrate and other constituents.

SEASONAL CHANGES IN THE NUTRITIVE VALUE OF YOUNG HERBAGE

It is frequently claimed by farmers that young autumn grass as milk-producing food is inferior to spring pasture grazed at the same stage of growth, but there is as yet no satisfactory explanation of this difference. Minson *et al.* (1960) have found that the digestibility of ryegrass and

cocksfoot cut at monthly intervals is slightly lower in the autumn than in the spring despite a higher leaf lamina percentage This is probably related to the markedly lower content of soluble carbohydrates which Waite and Boyd (1953) found in the purely vegetative growing points of autumn grass when compared with spring grass in which flower initials were developing It is possible also that these differences might affect the pattern of rumen fermentation

However, in experimental comparisons of spring and autumn grass cut at the same stage of growth and artificially dried, insignificant differences in milk production have been found (Holmes, 1956) and it is possible that differences in the field may be due to the depressing effect of environmental factors, such as contamination with mud or fungal infections, on the voluntary intake of the autumn herbage

On the other hand there is some evidence that the effect of season on the animal may be of importance Raymond *et al* (1954) examined the seasonal trends in the digestibility of the same batch of frozen herbage and found a small but consistent decline between autumn and winter, followed by an increase during the summer Workers in Western Australia have also found, in sheep on constant rations, a highly significant seasonal variation in the numbers of rumen bacteria The peak in bacterial numbers occurs in the spring and the minimum in late autumn, and Underwood and Moir (1956) have suggested a possible relation between light environment and rumen environment which could affect the efficiency of food utilization

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CHAPTER FIVE

Forage Crops

M. E. CASTLE

Introduction—Root crops: turnips and swedes, mangolds and beet, carrots, parsnips, potatoes—Forage crops: kale, cabbage, rape, mustard, maize, lupins—Buckwheat and cereals—Forage farming.

The crops to be discussed in this chapter include the forage and root crops grown primarily for stock feeding, the by-products of certain root crops grown for human consumption, and other miscellaneous crops which may, at times, be fed to farm livestock.

The forage and root crops, often termed succulent fodders, contain from 70 to 90 per cent moisture and are therefore relatively expensive to grow and handle. The majority of these crops are of value for only one season, and, unlike grass and clover, once grazed they do not produce a second crop. However, they do possess many of the advantages of herbage, and in addition, provide valuable food when grass is scarce, e.g. in the winter and early spring months. Although increasing emphasis is being placed on grassland and grassland conservation crops, a considerable acreage of forage and root crops is still grown. The root crop has been the pivot of successful and healthy rotations for many years and a departure from traditional cropping systems requires careful consideration. Hall (1953) in a discussion of this subject suggests that our approach should be to modernize our old-established methods and thus lower production costs. With this ideal in mind the crops described in this chapter can be usefully and safely integrated into a system of alternate husbandry in which cheap nutrients are produced from the grassland, and, when this is ploughed under, the soil

has an increased potential for producing arable crops for both animal and human consumption

The acreage in England and Wales of the more important root and forage crops is given in Table 5 1 It will be seen that whereas the

TABLE 5 1 *Acreage of root and forage crops (1,000 acres) England & Wales*

	1939	1944	1958	Percentage increase (+) or decrease (−) 1939 to 1958
Turnips and swedes	396*	471	234	−41
Mangolds	210	300	142	−32
Cabbage, kale, savoys and kohlrabi	94	196	354	+276
Rape	52	150	104	+100
Fodder-beet (high dry-matter content)	—	—	12	—

* Includes some for human consumption

acreage of turnips, swedes and mangolds has declined by over one-third since 1939, the area sown with cabbage, kale and rape has increased threefold in the same period.

The crops referred to in this chapter may be divided into two groups according to the part of the plant that is of greatest importance as a source of food for stock. Firstly, there are the 'root' crops (turnips, swedes, mangolds, beet, carrots, parsnips and potatoes), in which the root, tuber, hypocotyl, corm, or rhizome is used for feeding, and, secondly, there are the forage crops (kale, cabbage, mustard, cereals for winter grazing, rape, maize, lupins and buckwheat) in which the leaves and stems are eaten by stock. There are important nutritional differences between these two groups The 'root' crops may be regarded as sources of energy, for although they contain little fat, the sugar and starch contents of their dry matter are very high and their fibre, mainly in the outer skins, is largely cellulose and hemicellulose and is, therefore, well digested by ruminants

The protein value of 'roots' is poor both quantitatively and qualitatively, and their mineral value is low Their vitamin C content is often high but the much more important carotene content is very variable The forage crops, on the other hand, generally contribute

much more protein to the diet, are high in vitamins, particularly carotene, but frequently contain indigestible lignins, and, in terms of dry matter, often have a lower value than 'roots' as a source of carbohydrates.

The yields of nutrients from the various forage and root crops compared with those from grassland are presented in Table 5.2. It will be seen that grassland under fertile conditions and good management can produce more protein per acre than any other crop, but that a good crop of kale may equal it as a producer of starch equivalent. Both mangolds and fodder-beet have high yields of starch equivalent but are poor sources of protein compared with the kale crop. Many crops of kale exceed the level of production given in Table 5.2 and kale may be regarded as one of the highest producers of starch and protein on the farm.

TABLE 5 2. *Yields of nutrients from grass and various forage and root crops*

	Yield tons/acre	Dry matter cwt/acre	Starch equivalent cwt/acre	Protein equivalent cwt/acre
Good grass without fertilizer	10	40	24	4·5
High-producing ley* (S23+S100)	19	74	44	8·9
Kale, marrow-stem* (good crop)	25	75	44	6·5
Kale, marrow-stem (average crop)	15	45	26	3·9
Turnips and swedes (average crop)	12	28	18	1·7
Mangolds (variety Yellow Globe)	27	58	36	2·2
Fodder-beet (high dry-matter content)	16	64	38	1·9
Potatoes	8	40	30	1·4
Maize (green crop)	15	60	27	2·4

* Davies (1949)

The estimated cost of producing starch equivalent from different forage crops and from grassland is given in Table 5.3. These values, taken largely from the work of Hamilton (1955), clearly show the relative cheapness of grazing as a source of starch equivalent. They

TABLE 5 3 *Estimated cost of starch equivalent (1954 values) from crops and grazing*

	Cost of starch equivalent (£/ton)	Relative cost (grazing = 100)
Grazing (effective production)	11	100
Kale (grazed)	17	136
Kale (cut)	18	164
Fodder-beet (roots)	33	300
Cabbage	35	318
Turnips and swedes	36	327
Mangolds	40	364

also show that apart from pasture, both grazed kale and cut kale are cheaper than any of the other crops The period during which grazing of high quality is available in appreciable quantities is limited with even the most skilful management, and the importance of the kales, grazed if possible, is evident The cost of producing grass silage is the same as that of grazed kale and the silage may be preferable to kale under certain conditions Without exception, all the home-grown foods in Table 5 3 are cheaper per ton of starch equivalent than purchased cakes or meals

The cost of producing protein equivalent from forage and root crops follows a similar pattern to that for starch equivalent (Long, 1952) The cheapest source is temporary grass followed in order by, grass silage, kale, cabbage, swedes and mangolds

In addition to considering the yield per acre and the cost per unit of starch and protein equivalent it is of importance to know the amount of labour required for crops in relation to their starch equivalent value Some typical values quoted by Holmes (1953) are given in Table 5 4

TABLE 5 4 *Man hours required for various crops* (Holmes, 1953)

	Typical man-hours per ton	cwt S.E /ton	Man-hours per cwt S.E
Silage	2–4	2 4	1 25
Hay	10–15	7 2	1·74
Dried grass (tray drier)	25–30	10 4	2·64
Oats	35–40	12·0	3 12
Swedes	6–8	1 5	4·66

These figures indicate that grass crops require the lowest amount of labour per unit of starch equivalent and that swedes, a typical root crop, require the highest.

Furthermore, the labour demand for root crops is concentrated into peak periods, one of which occurs in early summer when labour is needed for silage and haymaking. This is a strong argument against having a large area of roots if the maximum use is to be made of grass-land. The month of the year during which the root and forage crops are available for consumption and the approximate dates of sowing are indicated in Fig. 5.1.

ROOT CROPS

cattle and sheep In the past, large rations of swedes were regularly fed to fattening bullocks up to 150 lb per day plus straw and a small weight of concentrates Such a system gave live-weight gains of up to 3 lb per day but was heavy on labour and could not be used economically today Where swedes are fed at present they generally constitute a portion of the maintenance rations of dairy cattle or growing stock Ewes in lamb will consume about 7–10 lb and fattening sheep up to 20 lb of swedes per day according to the size of the sheep For most feeding purposes, swedes are preferable to turnips although

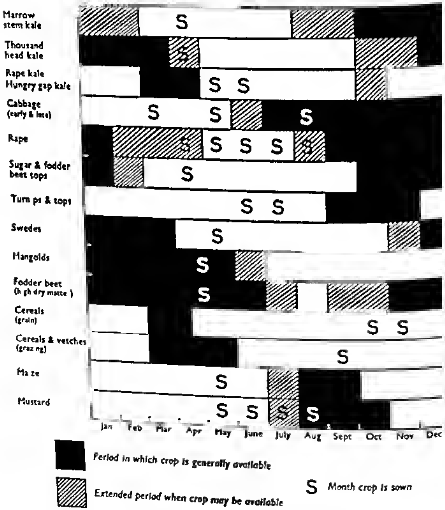

FIG 5 1 Availability of root and forage crops in the different months of the yea

turnips are rapid growers and can often be grown as a useful catch crop. Compared with kale and cabbage, there is little or no carotene in either crop and their mineral content is low (Table 5.8). If swedes have been harvested and clamped in the autumn the tops are a further source of useful stock food. Although not as important an item as sugar-beet tops, they can, nevertheless, contain up to 15 per cent digestible crude protein in their dry matter. They can thus be fed to either cattle or sheep in a similar way to kale. A ration of half kale and half swede tops reduces the chance of a milk taint and is preferable to one consisting entirely of tops. The yield of tops per acre is low and they cannot be considered a food of major importance.

Kohlrabi (*Brassica oleracea* sp.) are a form of cabbage with a thickened turnip-like stem which stands above, but close to, the ground. With a dry-matter content of 13 per cent, they resemble the swede in feeding value and may be fed to sheep, cattle and pigs. The crop stands frost fairly well and may be left growing in the field until required for feeding. Alternatively they may be lifted and stored like swedes. Unlike swedes they do not taint the milk. Also, because they protrude above the ground, there is little waste when folded with sheep. Although capable of withstanding conditions of drought, they are not a widely grown crop because of their low yield per acre.

(2) The *fodder sugar-beets* have a range of dry-matter content from 15–20 per cent and originate from crosses of sugar-beet with mangolds

(3) The *Barres-type mangolds* have a dry-matter content not exceeding 15 per cent

There can, however, be no absolute line of demarcation between the groups as nearly every gradation exists in the large number of varieties, and also any one variety may vary widely in dry-matter content from season to season. For example, Castle, Foot and Rowlands (1952*a*, *b*) found a range from 16 1 to 23 1 per cent dry matter in the same variety in different years although grown under very similar conditions A heavy top dressing of nitrogen may also be found to depress the dry-matter content of the root A uniform nomenclature has not been accepted in this country and often farmers are not sure which type they are growing and feeding Thus in a survey by Rodger (1952) the majority of farmers did not know the variety they were growing and 67 per cent of the beet surveyed was unidentified Because of this uncertainty much fodder-beet has been wrongly and uneconomically fed Generally, the varieties highest in dry matter (over 20 per cent) should be fed to pigs and the ones lower in dry matter to cattle

The value of fodder-beet as a food for fattening pigs on the Lehmann system has been shown by Braude and Mitchell (1949) and Dunkin (1952) Between 5 and 6 lb of beet can replace 1 lb of pig meal and up to 3 cwt of meal can be saved per pig The best results are obtained with a beet of high dry matter but since it is primarily a carbohydrate food, low in protein, minerals and vitamins the ration must be adequately supplemented in these respects Labour costs are higher than with an all-meal ration, but when the saving of meal is vital, this crop may be extremely useful The folding of dry sows on fodder-beet with the aid of an electric fence can save much labour if soil conditions permit The supplementary feeding of 2 5 lb per day of pig nuts containing 15 per cent of fish meal is suggested by Bolton (1954), but precise information on this relatively new technique is lacking and there is little available information on suitable amounts for breeding stock.

As a cattle food, fodder-beet has much to recommend it (Castle, 1953) It is extremely palatable to cattle of all ages and has been used successfully as an appetizer for sick cows In cattle-feeding trials in this country the value of each dry-matter unit of fodder-beet was found

to be slightly better than that of mangolds (Bailey, Castle and Foot, 1953), but for all practical purposes they may be considered as equal. If, therefore, fodder-beet is substituted for mangolds or other roots in the rations of cattle, it must be done on the basis of the relative dry-matter contents of the two roots. A normal ration of beet for a 10–11 cwt. dairy cow is 25–30 lb. per day although typical Danish rations may include up to 90 lb. per day (Young, 1952). This high level of feeding can easily lead to unbalanced rations and is not to be recommended. Boyle (1952) states that where beet comprises a high proportion of the ration of dairy cows there may be a slight lowering of the butterfat content of the milk. At reasonable levels of feeding, however, and where the ration is properly balanced for protein, minerals and vitamins, this drop is avoided.

The value of fodder-beet for fattening cattle has been shown by Dodsworth (1955). Steers eating 40–70 lb. of fodder-beet a day gained 1·73 lb. per day compared with a similar group eating 66–90 lb. of swedes which gained only 1·39 lb. per day. This was attributed to the fact that the steers on the ration of fodder-beet ate more dry matter per day than the animals on the ration of swedes.

A number of reports of digestive disturbances and even deaths in cattle as a result of feeding fodder-beet have been reported (Worden, Bunyan and Pickup, 1954; Penny, 1954). 'Beet poisoning' as it is generally termed in Denmark, is sporadic in occurrence and is a loose term which describes a number of varying types of digestive and metabolic upsets in cattle. Occasionally it may be due to an excessive consumption of adherent soil and this emphasizes the importance both of growing a variety of beet with a low dirt tare, and of cleaning the roots. Digestive disorders have also resulted when varieties from low dry-matter strains have been fed before a long enough period of maturation has elapsed after harvest time.

Varieties of high dry-matter content can usually be fed immediately after harvesting, but even then care should be exercised in a mild season when growth continues up to the time of pulling. The ratio of non-protein nitrogen to total nitrogen is highest in the lower dry-matter varieties (Table 5.5.) and this may be the reason for the longer period of maturation between harvesting and feeding which is necessary for this group. Also, the lower the dry-matter content of the root the higher is the total nitrogen content of the root dry matter. The condition described by Worden *et al.* (1954) was a hypocalcaemia-like syndrome resembling milk fever and resulted from the consumption

TABLE 55 *Dry matter and protein contents of four types of roots—1950 trial* (Castle Foot and Rowlands 1952b)

Type	Variety	Dry matter content of root (%)	Crude protein content of root dry matter (%)	True protein content of root dry matter (%)	True protein as % of crude protein
Mangold	Yellow Globe	10 6	6 2	3 6	58
Mangold (Barres type)	Barres Øtofte	15 6	5 1	3 2	63
Fodder sugar beets	Red Øtofte	19 0	4 4	2 8	64
Fodder sugar beets	Pajbjerg Rex	22 6	4 3	2 9	68

of about 40 lb per head of fodder-beet which had been suddenly introduced into the ration In practically every similar case there has been a sudden change of diet involving the feeding of the beet Therefore even if the stock have been on a ration containing another type of root, fodder-beet should always be introduced slowly into a ration over a period of at least ten days An account of sugar-beet poisoning in cows by O Connor (1951) is again characterized by the fact that the affected animals suddenly ate beet from a clamp awaiting dispatch to the factory The main symptom was difficulty in rising, and a severe reduction in milk yield

Cases have been reported of sheep and cattle dying as a result of eating mangolds (Snyders 1945) and Scarisbrick (1954) found an acid indigestion in sheep when a ration of 12 lb of mangolds per day was inadvertently increased to 15 lb This was attributed to an abnormal level of lactic acid in the rumen which usually does not accumulate in large quantities Danish opinion is that the higher the dry-matter content of the root the more probable is the chance of a feeding disorder For this reason varieties with a dry-matter content of 17–18 per cent are preferred for cattle feeding to those with higher values

The tops of both sugar-beet and fodder-beet may provide food for livestock. In practice they vary considerably in nutritive value depending on the proportion of leaf to crown the length of time between topping and feeding and contamination by soil Sugar-beet tops always have a portion of crown attached to the leaves whereas the fodder beet are generally all leaf and because of this the crude protein content of the dry matter of the fodder-beet tops is usually higher than that of the sugar-beet tops Crude protein contents of up to 21 5 per cent have been recorded in fodder-beet tops from a crop

which has had a heavy top-dressing of nitrogenous fertilizer (Castle, Foot and Rowlands, 1952*a*). Contamination of the tops with soil can seriously lower their digestibility (Steensberg and Winther, 1948), whilst in certain circumstances, the contamination may reach such high proportions as to cause the death of sheep (Rayns, 1945). Dependent, therefore, on the above factors, the tops can be equal on a weight for weight basis, to either kale or swedes. Unwilted sugar-beet tops contain approximately 1 per cent oxalic acid and are thus a laxative food when fed to livestock. If wilted, the concentration of oxalic acid is reduced, but a further safeguard before feeding is to add 2 lb. precipitated chalk per ton of tops. This combines to form insoluble oxalates which are harmless to stock and therefore scouring is reduced. Woodman and Bee (1927) suggest that the oxalic acid may render not only the calcium in the tops unavailable but some of the calcium in other foods which may be fed with the tops. Thus the feeding of chalk, although not in excess, may be doubly valuable particularly for pregnant milking animals. A severe scouring in cattle occurs regularly every season in Germany in the sugar-producing districts when the cattle are almost entirely maintained on a diet of beet tops (Plaas, 1950). The oxalic acid theory is rejected by Plaas, who suggests that the excess of lactic-acid-forming bacteria on the leaves of the plant upsets the balance of the flora in the digestive tract and excess lactic acid is produced which irritates the intestinal wall.

The feeding of untopped fodder-beet to cattle in the autumn has occasionally been tried in this country, but even from the limited information available, the need for great caution is apparent. Although the proportion of tops to total plant is about one to four or five on a dry-matter basis the tops are not usually wilted and scouring occurs.

Beet tops may impart a fishy taint to milk due to the presence of betaine which gives rise to either trimethylamine or its derivatives. They should, therefore, be fed with care—preferably out of doors after the morning milking.

Mangolds are the member of the family with the lowest dry-matter content, having values ranging from 9 to 15 per cent. They may be fed to all classes of stock and provide a valuable source of carbohydrates. When harvested in autumn 40–70 per cent of the total nitrogen in the crop is in the form of non-protein nitrogen. A high proportion of nitrate is present and since this would cause scouring among livestock, the crop is normally stored for several months prior to feeding to allow most of the nitrate to be reduced to less toxic compounds. Mangolds

are normally fed after Christmas A severe outbreak of mangold poisoning in pigs involving two hundred deaths was reported by Robinson (1942) in New Zealand Freshly pulled mangolds had been cooked with the result that the nitrate had been converted into nitrite, and when fed, had toxic effects Turnips, swedes and sugar beet have all been involved in similar cases and it is wise not to feed pigs these boiled roots or the water in which they have been boiled

A daily allowance of about 40 lb of mangolds is suitable for inclusion in the ration of a 10–11 cwt cow, and unlike many of the root crops previously discussed they will not produce any taint in the milk.

As indicated in Table 5 3, mangolds are a relatively expensive source of carbohydrate and are thus not now fed in the exceedingly large amounts which were used in the past Sheep are never folded on mangolds since before the roots would be ready for use they would almost certainly be damaged by the cold weather Mangolds from a clamp are, however, commonly fed to sheep running on pasture and in spring they are useful as a source of carbohydrate to balance the high-protein grass Pigs will eat mangolds greedily, but, owing to their low dry matter and bulky nature, mangolds are not as useful as fodder-beet or potatoes in fattening rations for pigs This is shown in Table 5 6 which summarizes a trial in which two similar groups of

TABLE 5 6 *Average live-weight gain and food consumption per pig* (Braude and Mitchell, 1949)

Ration	Initial weight (lb)	Wt after 119 days (lb)	Weight gain (lb)	Daily wt gain (lb)	Food (lb) consumed/lb of live-weight gain	
					Meal	*Roots*
Meal+mangolds	58 7	169 2	110 5	0 93	2 69	16 2
Meal+fodder-beet	58 3	209 7	151 3	1 27	1 97	9 0

pigs each received the same basic high-protein meal ration of 2 5 lb per day, but the ration of one group was supplemented with mangolds (9 1 per cent dry matter) and the other with fodder-beet (21 3 per cent dry matter)

The growth rate and efficiency of food conversion of the fodder-beet group were much superior to those of the mangold group as the bulky nature of the mangolds limited the intake of nutrients

Mangolds contain oxalic acid which is normally rendered insoluble, and therefore harmless, when the mangolds are maturing in the clamp. Under certain conditions, not as yet clearly defined, insoluble calcium oxalate is thought to be deposited in the urethra and bladder, and urinary calculi develop in the male lambs and bullocks. Halnan and Garner (1953) consider that this arises when the mangolds have been grown on chalk soil although Forsyth (1954) incriminates roots from lime-deficient soils. The experimental evidence is also conflicting. Wethers (male castrated sheep) fed potassium oxalate at the rate of 1 gm. per 6 lb. live weight for 6 months remained perfectly healthy (Anon., Report of Dept. Agric. Queensland, 1951) whilst a daily dose of 30 gm. oxalic acid to a young calf produced signs of disturbance in the urinary tract on the fortieth day after dosing began (Thomas and Prier, 1952). A new concept of the aetiology of this condition as a result of ultra-microscopic studies of urine by Puntriano (1954) postulates that the colloid and crystalloid balance in the urine may be influenced by both mineral and fluid intake. The trouble is not very widespread but, where male animals are being fed mangolds, the amounts should be kept in moderation and the sprouts must always be removed.

CARROTS AND PARSNIPS

These two crops are rarely grown for stock feeding. If, however, prices are low and there is an excess of the crop, some may be available for feeding to animals.

Carrots (*Daucus carota*) have a dry-matter content of about 13 per cent, and a higher feeding value than most varieties of mangolds and swedes. They are relished by horses of all ages and may also be fed with safety to cattle, sheep and pigs. They have a high carotene content, and, when fed to dairy cattle, will improve the colour of the milk in winter time. White varieties of carrots which are very occasionally grown have a feeding value lower than that of the red type.

Parsnips (*Pastinaca sativa*) have a higher feeding value than carrots, and for many years they have been used for feeding dairy cattle in the Channel Islands (Moore, 1943). Pigs and poultry will also eat them. Parsnips should not be confused with the tuberous roots of Water Dropwort (*Oenanthe crocata* L.) which are extremely toxic to livestock.

Both carrots and parsnips should replace swedes or other roots in rations on a basis of equal weight of dry matter. The tops of both carrots and parsnips can be fed to livestock with safety.

POTATOES

Potatoes (*Solanum tuberosum*) are a further crop which in this country is mainly grown for human consumption, and only surplus, undersize, or diseased tubers are used for livestock feeding. Such surplus potatoes are best utilized by pigs and poultry. For pigs under intensive fattening conditions the potatoes are best cooked before being fed (Braude and Mitchell 1951) and 4.7 lb of potatoes will replace 1 lb of pig meal. Under extensive conditions of pig feeding where time, labour and running costs are not of primary importance, raw potatoes can be fed satisfactorily. In both cases, however, 2–3 lb of a well-balanced meal should be fed daily in addition. Raw potatoes must be fed to cattle with caution. They should be clean, preferably sliced to guard against choking, and slowly introduced into the ration. Cattle 'blow' quite easily when fed raw potatoes and 20 lb per day is a safe maximum. They may also induce excess salivation which in the cowshed fouls the troughs and causes an unpleasant odour. In some recent Dutch work (Dammers, 1954) the feeding of steamed potatoes to dairy cattle decreased the butterfat content of the milk by 0.08–0.20 per cent whereas, in three out of four trials the feeding of raw potatoes increased it. Sheep will eat 2–4 lb of raw tubers a day and old records provide abundant evidence of the use of potatoes for this species (Robinson, 1949). Potatoes, fodder-beet and crushed oats have been fed to in-lamb ewes on grass during the last few weeks prior to lambing as a precaution against pregnancy toxaemia.

Raw potatoes have a laxative effect and raw diseased tubers are likely to produce digestive upsets and should never be fed. When potatoes turn green on exposure to sunlight, solanine, a poisonous alkaloid, is formed. Green sprouts may contain up to 5 per cent of this alkaloid and, because of their danger to livestock, they should always be removed before feeding the potatoes. Green tubers can be rendered safe by storing in total darkness for two weeks or more until the green colour disappears (Forsyth, 1954). Alternatively, they should be boiled, and the water discarded, before feeding.

Potato haulm has a low feeding value and is dangerous because of its content of solanine. Its use as a feeding stuff is virtually nil, but occasionally it is cut prior to wilting and ensiled. Even when made into silage, care must be taken when introducing this food into animals' rations (Dijkstra, 1945).

Where potatoes are grown for commercial manufacture, e.g. the production of starch, the potato residue is a useful food-stuff for cattle

The residue stores well in airtight silos and in Holland 20–30 lb. per day are commonly fed as a source of supplementary carbohydrate to milking cows on high-quality grass. The dry-matter content averages about 16 per cent and from 40 to 60 per cent of the dry matter is starch. Potatoes can be successfully ensiled between layers of grass or other green crops in a silo. The heat from the fermenting silage will cook the potatoes, and a mixture of one part of potatoes and three of green crop has proved to be suitable.

FORAGE CROPS

KALE

There are four types of kale (*Brassica oleracea* sp.) commonly grown for livestock feeding: marrow-stem kale, thousand-head kale, hungry-gap kale and rape kale. The first two are the most widely grown, and the marrow-stem type, either sown alone or with another brassica crop, is without doubt the most popular at the present time. If well cultivated and properly fertilized, both marrow-stem and thousand-head can produce high yields of nutrients (Table 5.2) at costs which compare very favourably with other alternative winter fodders (Table 5.3).

Although the feeding value of kale is rightly regarded as being high, it is subject to wide fluctuations due to factors such as season, proportion of leaf to stem and fertilizer treatment. This is of importance in balancing rations if the maximum use is to be made of this crop and the stock are to be fed correctly. The leaf of kale has always a much higher protein content than the stem (Table 5.7) and hence changes in the leaf-to-stem ratio due to leaf fall in the winter months can greatly alter the feeding value of the crop.

TABLE 5.7. *Crude protein content* (%) *of the dry matter of kale leaf and stem* (Castle, Foot, Hosking and Rowlands, 1957)

(4-year average)

	Marrow-stem Leaf	Marrow-stem Stem	Thousand-head Leaf	Thousand-head Stem
No added nitrogen	20·8	9·4	19·9	11·0
Plus 6 cwt/acre sulphate of ammonia	23·9	13·9	23·2	13·2

The effect of the top dressing of nitrogenous fertilizer can also be observed from Table 5 7 Because of its leafy nature kale is a particularly valuable source of carotene for livestock in the winter months and helps to maintain the colour and vitamin-A potency of the milk. As with the protein the carotene content of kale is also subject to a wide variation In Sweden, Kivimae (1950) analysed samples of kale at weekly intervals and noted a decrease from 105 to 60 mg of carotene per kg from the beginning to the end of the season He suggested that this may be attributable to decreasing temperature, especially to night frosts The vitamin-C content of kale is also high, although swedes are superior in this constituent Kale is rich in minerals (Table 5 8) and, compared with some of the traditional roots which it

TABLE 5 8 *Mineral co pos t on (%) of kales swedes and ma igolds* (Woodman 1948)

	Total ash	Lime (CaO)	Phosphoric acid (P_2O_5)	Ratio CaO–P_2O_5	Potash (K_2O)	Chlorine (Cl_2)
Marrow-stem kale	1 9	0 43	0 12	3 6	0 55	0 21
Thousand-head kale	1 7	0 39	0 13	3 0	0 52	0 16
Swedes	0 7	0 08	0 08	1 0	0 30	0 04
Mangolds	0 9	0 02	0 09	0 5	0 45	0 16

has replaced in rations has a very high calcium content This characteristic would seem particularly important if such home-grown forages as clover and lucerne are also incorporated in the ration since these are also high in calcium and would accentuate any mineral imbalance The provision of fresh green kale for as many months as possible in winter could do much to improve the low plane of nutrition especially in protein which may result in anoestrus in heifers and even in adult cattle

The presence in kale of some goitrogenic factor has been reported by Shand (1952) Attention was first drawn to this on a farm in which thyroid enlargement and neonatal deaths occurred in lambs after a winter in which pregnant ewes had been fed almost exclusively on kale from September to January An attempt to reproduce this disorder another year almost entirely failed and indicates that the activity of goitrogens may vary not only from area to area but also from season to season.

It has been reported that the feeding of kale may result in a type of poisoning which is characterized by haemoglobinuria (red water) in cattle (Gregor, 1952), and a haemolytic anaemia with jaundice in sheep (Stamp and Stewart, 1953). With the cattle this condition occurred suddenly, and in one herd eleven out of twelve animals were affected. Although they appeared to be very ill, were extremely dull and lacked appetite, they recovered in 3–5 days once the kale feeding stopped. Rosenberger (1943, 1950) has described a similar condition in Germany, termed kale anaemia, which may even cause death and which results from the consumption of large amounts of kale, 90–110 lb. per day, for a prolonged period. The highest producing and the pregnant cows were chiefly affected and haemoglobinuria was frequently the first and most striking symptom. It was suggested that a weight of 33 lb. of kale per day should not be exceeded if the kale is to be fed for long periods. It is thought that outbreaks are commoner during periods of wet inclement weather than in dry weather (Gregor, 1952). Parkinson and Sutherland (1954), describing outbreaks of post-parturient haemoglobinuria in dairy herds, found that the condition occurred mainly in areas where cattle were known to be affected with a phosphorus deficiency. The ingestion of a cruciferous plant, such as turnips, precipitated the disease but the authors suggest that aphosphoris is a necessary predisposing factor. Anaemia and haemoglobinuria in dairy cattle has been attributed by Angelo (1951) to the consumption of seeded wild cabbage (*Brassica oleracea* Linn.), but in this case the causative factor was thought to be in the seed. The feeding of frosted kale can cause a similar condition (Evans, 1951). Generally cattle may safely consume kale which has frost on the leaves (frozen kale) without ill effect, but they should not be fed kale which has been substantially damaged by frost (frosted kale) (Trinder, 1953). Because of the loss of kale leaf due to frosts, the feeding value of the crop declines and it is generally considered safer and more economic to have the bulk of the marrow-stem and thousand-head kale eaten before the severe frosts begin. Certain strains of thousand-head kale are winter hardy, but the danger from frosted kale could still arise.

A typical ration which would supply nutrients sufficient for the maintenance of a 10–11 cwt. cow and the production of 1·5 gallons of milk per day is: 17 lb. of hay plus 50 lb. kale. Kale is a particularly useful complement to straw and poor hay, and will supply the protein, minerals and vitamins which the coarse fodders lack, and hence improve the value of a mixed ration.

The practice of folding cattle on kale has increased rapidly in the last few years since the development of light-weight pottable electric fence equipment (Castle and Foot, 1949) By the use of this type of equipment the cost of feeding kale has been reduced as cutting and carting are eliminated In general the method has much to recommend it, and by daily strip-folding, the herd's intake can be rationed, although individual animals may eat considerably more than others Where possible, a minimum of three yards of frontage should be allowed for each cow to prevent congestion along the fold wire which can easily result in bullying, horning and waste of the crop It is advantageous to have stock without horns Folding is normally done after the morning milking, and within two hours after entering the fold the cattle will cease grazing and lie down (Castle, Foot and Halley, 1950) The cattle should, therefore, have access to an old ley or stubble on which to rest in comfort until the next milking If the animals are forced to stay on the kale stubble they will not only get dirty but may also damage their feet This is particularly prone to happen in frosty weather The damage may occasionally result in foul-of-the-foot infection, and on very flinty soils there have been reports of grazing having to be abandoned because of lameness and a consequently lowered milk yield.

In a survey carried out in south-west England (Connold, 1952) a quarter of the farmers stated that they had experienced bloat when their cows were grazing kale, and in isolated herds this problem had been so serious that the practice had either been abandoned or extreme measures, such as the wilting of the kale before feeding, had been adopted. A more detailed study of this survey (Connold, 1951) revealed no positive relationship between the incidence of bloat and such factors as the use of various quantities of nitrogen on the crop, variety of kale, rainfall or soil type Where the grazing of the kale was controlled by time rather than by limiting the area, four out of ten affected herds were only grazing for one hour or less The feeding of hay, straw, or other roughage before grazing kale and the keeping of stock from frosted crops is to be recommended Although kale is a succulent crop, dairy cattle drink regularly when folded, and it is advisable to have water available

Kale is a palatable food for all classes of stock and may be fed safely to poultry, pigs or horses Poultry will eat both the kale leaf and the marrow inside the stems if they are split It should not be fed in large amounts, but as a source of minerals, vitamins and, to a lesser extent,

of sugars, it may be a useful supplement for intensively housed birds. Also where a regular daily allowance of fresh green food is necessary for pigs, e.g. for pregnant sows, or boars kept in yards, kale is again useful. It is too bulky for feeding in large amounts to fattening pigs although weights of up to 14 lb. a day may replace 2 lb. of meal in the rations of fatteners. As the stems are often not eaten, this should be allowed for when weighing the ration of kale.

Apart from the goitrogenic factor already mentioned, kale is safely and widely used for sheep feeding. As a crop for folding it has the advantage that its edible portions are well above ground level, and, therefore, remain clean, although many of the leaves are pulled off and trampled underfoot when folding takes place. The crop should not be allowed to become too coarse since the stems will be rejected and the utilization of the crop will be low. Store cattle are useful in clearing up such a crop. Fattening hoggs (yearling sheep) folded on marrow-stem kale from October onwards will eat about 13 lb. a day whereas a ewe with lambs will consume up to 20 lb. a day of thousand-head in the early months of the year. Hay and concentrates should be fed in addition.

Hungry-gap kale and rape kale are hybrid plants of extreme winter hardiness and, although low yielding, are of value when normal green crops are finished. Hungry-gap, in particular, is of use in late spring when all other kales are finished. A crop of hungry-gap kale sampled in the open winter of 1948–9 when leaf-fall was low, had 21·2 per cent crude protein in its dry matter (Watson and Smith, 1951).

TABLE 5 9 *The nutritive value of certain brassica crops*

	Dry-matter content (%)	Digestible crude protein (%)	Protein equivalent (%)	Starch equivalent (%)
Marrow-stem kale*	14 6	1 1	0 9	9 8
Thousand-head kale*	14 8	1 8	1 4	8 8
Cabbage drumhead†	11 0	1 1	0 9	6 6
Cabbage ox-heart†	15 3	1 8	1 5	9 5
Rape†	14 1	2 0	1 7	6 9

* Anon *I C I Bulletin No 5* 1955 † Woodman 1948

therefore, result in a ration which satisfied the animal's appetite but not its nutritional requirements When the dry-matter content of cabbage is similar to that of kale, the starch and protein equivalents are also similar (Table 5 9) and the two crops can be used in much the same way Between 50 and 60 lb a day are commonly fed to dairy cattle and up to 20 lb a day to sheep which are being 'flushed' or fattened. Cabbage have been grown recently as a 'tracker' crop between rows of kale to allow a clear run without earths for an electric wire The method, however, cannot be recommended, since the exact position of the electric wire cannot be forecast with accuracy, and the overall yield of crop is generally lowered

One drawback of cabbage is the risk of a taint in the milk if large quantities of the crop are fed to milking animals, and therefore it is advisable to feed it immediately after milking and preferably in the open air Pigs horses and poultry can all be fed cabbage with safety but because of its bulky nature its value is as a source of minerals and vitamins rather than as a source of carbohydrate or protein

Brussels sprouts, in times of glut, can also be fed to stock with success (Watson, 1949)

RAPE

As indicated in Table 5 1, the acreage of rape (*Brassica napus*) has increased rapidly in recent years For example in Wales the acreage increased four- or five-fold between 1939 and 1950 (Evans, 1952) This is due to a wider appreciation of its feeding value, its importance as a nurse crop in reseeding, and the fact that it is extremely useful as a pioneer crop on hill and marginal land (Ellison, 1943) It is practically the only crop that can be grown on marginal land which will fatten

lambs and, because of this, has great economic significance on this type of land. Rape is ready for grazing with either sheep or cattle about three months after sowing and, as with other quick-growing crops, has a tendency to be laxative. Its composition (Table 5.9) is similar to that of kale but has a narrower ratio of starch equivalent to protein equivalent. It is especially valuable for 'flushing' ewes as it is generally at an ideal stage of growth at mating time.

An acre of good rape will fatten 10–16 cast ewes, wethers or Black-faced lambs (Martin, 1955) and, to make the maximum use of the crop, younger rape should be fed to the lambs and the older and stronger rape to the ewes. Sheep taken from hill grazing should be given a short time on grass to prepare them for the change before putting them on such a high-quality food as rape. As rape is very liable to taint milk, excessive quantities should not be fed and it is preferable to graze it as long before milking as possible.

Various disorders of livestock occur sporadically when feeding rape. Cote (1944) has recorded four main types.

(1) A respiratory form, clinically very similar to fog fever.
(2) A digestive type with marked constipation, absence of ruminal movements and dullness.
(3) A urinary type characterized by haemoglobinuria.
(4) A nervous type with blindness.

syndromes observed included bloat, photosensitization and corneal opacity. These troubles with rape are, however, rare and the advantages of this crop heavily outweigh the risks involved.

MUSTARD

Two species of mustard (*Brassica* sp.) are commonly grown. White mustard as a forage crop for folding, and black or brown mustard for the production of seed for use as a condiment. The white mustard is useful as a rapidly growing catch crop and is often used for 'flushing' ewes at tupping time. The crop is commonly sown after early potatoes or on corn stubbles and should be grazed within six or eight weeks before it becomes rank and stemmy. It is also sown as a pioneer crop on poor hill land where it may be grazed with sheep. It is susceptible to frost and should, therefore, be used by early autumn. It is a safe food under the vast majority of conditions although Forsyth (1954) reported an isolated case of poisoning in a flock of lambs which he attributed to this crop. In this instance the mustard had been left ungrazed longer than usual and the pods had formed. At this stage, mustard oil may be formed in the seeds and the crop is also unsuitable for milking cows because of the danger of a taint in the milk. The mustard oil is a glucoside possessing a very pungent smell and taste. Black mustard is much more dangerous than white and there are records of poisoning among cattle, pigs and poultry which have eaten food contaminated with it. The symptoms are those of an irritant poison with intense colic, restlesmess and ultimate collapse.

The black mustard is not grazed but cut and harvested like a cereal. The chaff may be used for feeding (Moore, 1943) but the straw is of no value. Shed seed from this crop may foul the land and should be allowed to germinate before being killed by ploughing.

MAIZE

Maize (*Zea mais*) has been fairly widely grown in the south and east of England for use as a summer forage crop. In other areas the yield of maize is limited by the shorter growing season since this crop is particularly sensitive to frost in its seedling stage. After sowing, the dangers of depredation by wild birds is very high, but in a suitable growing season yields of 16–20 tons per acre of succulent material can be grown. This can be fed to cattle in the late summer when the production of grassland nutrients is low but it is expensive to handle and the crude protein content of the dry matter is rarely over 10 per cent. Except

for portions of the fibrous stems it is a palatable crop. As a silage crop for winter feeding, trials with varieties of American hybrid maize have not been very promising (Castle, Foot and Rowlands, 1951, 1952). Yields of dry matter and protein were low compared with those commonly obtained from a good kale crop or from a silage-cut from a well-managed ley. Bland (1953) has reported higher yields of dry matter per acre from eastern England, but again the production of protein was low. Varieties such as White Horse Tooth which are grown for feeding green are not suitable for silage making owing to their late maturity and lack of cob formation. Maize is rarely, if ever, fed to sheep, and in general it is not a suitable crop for integration into a system of intensive grassland and forage farming.

LUPINS

In Britain, the growing of lupins (*Lupinus* sp.) is confined almost entirely to the poor light land in the eastern counties although it assumes greater importance in New Zealand, Western Australia, South Africa and parts of Eastern Europe. Lupins are a leguminous crop which will grow on a sandy acid land which they enrich when ploughed in. Many sandy districts on the Continent which were practically valueless have been greatly improved in fertility by using these plants as a green manure (Percival, 1935). They can be divided into two main types, bitter lupins, either blue flowers (*L. angustifolius*) or yellow-flowered (*L. luteus*) and sweet lupins, generally yellow-flowered (*L. luteus*). The bitter varieties are preferably grown as soil improvers since there is always some risk of poisoning if they are fed to livestock. In spite of this, bitter blue lupins have been folded with sheep by taking the precaution of allowing the animals access to some other food at the same time and not allowing them on the lupins if they were very hungry. The sweet lupin is readily eaten by all classes of livestock, and lambs have been successfully fattened on the green crop. The danger lies in knowing whether a specific crop is of the sweet or bitter type, in order that the necessary precautions may

CEREALS

The cereal crops, wheat, oats, barley and rye are grown principally for the production of grain; only a small area is utilized for grazing purposes. Oats, or any other cheap available grain, are often sown at a rate of about one bushel per acre with grass and clover seed, when reseeding grassland directly. The cereals germinate rapidly and provide grazing for the stock whilst the ley is establishing itself. With good conditions of ley establishment and with mixtures containing quick-growing grass, such as Italian ryegrass, the value of the cereal is questionable. The spring grazing of autumn-sown crops of corn is a useful method of providing an out-of-season bite of green food. The feeding value of the cereal at this stage is high, and may be compared with that of leafy spring grass. It is less palatable to stock than spring grass, but at the time it is normally grazed, late February and March, grass is not normally available. This grazing has a stimulating effect on the milk yield of dairy cattle (Robinson, 1951) which is often much greater than that calculated from the extra intake of food nutrients and the crude analysis of the green crop. In such cases it is possible that the cereal may be oestrogenic. Rye, especially in the spring, was reported to be oestrogenic by Dohan, Richardson, Stribley and Gyorgy (1951). The object when cereals are being grazed should be to allow the stock to eat a given area in a period of 7–10 days, avoiding very hard grazing, and to take the animals off the crop by mid-April. Failure to do this may reduce the potential grain yield by 20–25 per cent. An application of 1–2 cwt. per acre of a nitrogenous fertilizer after the grazing will do much to reduce the loss of grain and will make the grazing an economical proposition. If this practice of cereal grazing is adopted it is important that the milking cattle should be able to follow it with an early bite from grassland or some similar crop. If not, milk yields will suffer a set-back.

Special autumn-sown crops primarily for grazing in early spring are based on rye, oats and vetches with or without Italian ryegrass. Such mixtures will yield from 2·5 to 3·5 tons of high-protein green food in late March and April and a small area will be extremely useful for stimulating milk yields of both cows and ewes at a time of the year when other forage crops are scarce. The cost of producing this relatively low-yielding special-purpose forage crop has to be charged entirely to the dairy herd or flock and in many cases alternative methods of producing nutrients from a grass crop are more efficient. An oat and vetch crop can be multi-purpose for grazing, ensiling, making

into hay or even harvesting as grain, depending on requirements at the time The sowing of a small acreage of winter rye and vetches is an old practice and with early sowing and a dressing of nitrogen in the spring, the crop will be ready for grazing much earlier than was usual in the past

In Great Britain the grazing of cereals is without any danger to the health of the animals but in New Zealand, particularly in South Island, lameness and associated unthriftiness in young sheep grazing green fodder crops has been known for a long time (Ewer, 1949) This condition only occurs in some winters and is a form of rickets Occasionally sheep grazing turnips or kale may show evidence of it but it is on Italian ryegrass or green cereals that the incidence is highest There is a pronounced hypophosphataemia and it appears that there is some specific principle in green cereals which interferes with phosphorus metabolism in growing sheep Grant (1955) has produced evidence that the rachitogenic factor is, in fact, vitamin A and that any of the plant carotenoid precursors could produce a rachitogenic effect The relative freedom from rickets of lambs wintered on mature foods and permanent pasture is probably accounted for by the fact that these foods contain a considerable proportion of dead leaves These, in contrast with the green material, have a relatively high vitamin-D content and a correspondingly low carotenoid content Vitamin D_2 given orally was found to be completely effective in preventing or rapidly curing the condition

The grazing of cereals by milking cattle has resulted in serious depressions of the butterfat content of milk in parts of New South Wales which on certain farms was of major economic importance (McClymont, 1950) This was shown to be due to a lack of roughage in the diet of the animals and could be remedied by the feeding of a fibrous food. Under conditions in this country it is very unlikely that grazed cereals would contribute a large part of the daily intake of nutrients for dairy cattle, but, as a result of Australian experience, such a diet should be balanced by feeding either hay or straw in addition

A condition known as wheat pasture poisoning occurs in parts of the Southern Great Plains of the United States when cattle are grazing wheat which is used as a temporary pasture crop in the autumn, winter and spring (Savage, Smith and Costello, 1948, Crookshank and Sims, 1955) The trouble increases during periods of lush growth and the animals principally affected are pregnant cows or cows suckling calves The symptoms are very similar to those of grass tetany, and if treat-

ment is delayed, there is little chance of recovery. Most cases occur after the animals have been on the wheat for over sixty days and there are indications that cattle given access to dry roughage before and during the grazing period are the least affected.

FORAGE FARMING

In the last few years a system of husbandry termed 'forage farming' has been practised on a small number of milk- and meat-producing farms. The system is based on sound rotational practice and land use, and the aim is for the livestock to harvest their own food, largely arable forage crops and short leys, for as much of the year as possible. For example, forage crops such as kale and rape are grown as cheaply as possible and then grazed *in situ* by means of the electric fence. Maximum use is made of the land by catch-cropping, cultivation costs are kept to a minimum, and the electric fence plays an important part in the rationing of the crops. In general, forage crops if well fertilized will produce high yields, and if they are cut and fed green, a high stock-carrying capacity can be maintained. For instance, the University of Leeds had a thirty-acre small-holding on which dairy cows were maintained on arable crops both summer and winter (Moore, 1943). One cow was carried on just over one-and-a-half acres of land, with a proportion of cake fed to the high-yielding cows. Although such a system may not be economically practicable at the present time, because of the high cost of labour, it does indicate the potentialities of forage cropping. With improved methods of grazing the crops *in situ*, the method has interesting possibilities.

for grazing kale or other forage crops *in situ* when grass is not available. Forage farming, if skilfully integrated into a broader system of grassland husbandry can help to reduce overall costs in the provision of nutrients at difficult times of the year. It can rarely offer an economic system of complete self-sufficiency on the small farm

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CHAPTER SIX

The Nutritional Value of Conserved Products

S. J. WATSON

Introduction—Artificial drying—Natural drying—Ensilage.

The products of conservation of forage crops and grass, using the word in its widest sense, are the results of two main processes. The first involves desiccation and may be rapid as in the case of what is called tificial drying, or prolonged in the natural drying of the crop to give ay. The second process is that of ensilage and depends on the con- olled fermentation of a crop of relatively high moisture content.

The plant, more particularly if it is young and leafy, is in a state of ctive metabolism and after it is cut there will continue to be changes ntil such time as the cells of the plant actually 'die'. Most of the nformation that is available on these changes is based on the general groups into which the agricultural chemist normally divides the con- stituents of the crops, namely moisture, crude protein, ether extract, crude fibre, nitrogen-free extractives and ash or mineral matter.

Modern work, using techniques such as paper chromatography that have so greatly extended our knowledge of the compounds within these general groups, is adding considerably to our knowledge of the fate of the individual substances found in the plant. In the fresh crop biological processes continue actively after cutting and many of the changes are so rapid that is is very difficult indeed to obtain a sample that is truly representative of the crop at the exact moment it is cut. This whole subject has been reviewed by Watson (1952) and it is quite certain that, if a true sample is to be obtained, special rapid treatment is essential for the inactivation of all biological processes (Laidlaw and Wylam, 1952).

The most obvious change that happens after cutting is the loss of moisture, a physical process of variable length, during which it must be realized that many chemical changes will also take place. Greenhill (1933), for example, showed that during the drying of samples of herbage in shallow trays in a drying room operating at 40° C. there might be a loss of as much as 20 per cent of the original dry matter in 48 hours.

At a much later date Ekelund (1949) found losses of dry matter during drying of the order of 8 per cent with clear evidence of the breakdown of the constituents of the carbohydrate fraction of the crop. He also found evidence of reverse changes with the build-up of simple sugars to more complex forms. Macpherson (1952) at Edinburgh has obtained evidence of the rapid breakdown of the protein fraction of grass shortly aftet cutting. The breakdown is very rapid in tbe presence of sufficient moisture and the extent, as might be expected, is related to the speed of desiccation of the hetbage. An equilibrium seems to be established when a dry-matter content of between 40 and 50 per cent has been reached. These changes may be ascribed to enzymic action since in the early stages the bacteria on the herbage do not seem to be operative. Wylam (1953) in the same laboratory has sbown evidence of considerable enzymic breakdown of the sucrose and fructosan in grass to simplet compounds during wilting. The nature of the changes that take place most obviously depends upon tbe actual chemical compounds present at different stages in the development of the crop. These will vary with many factors as has already been seen in earlier chapters.

The most obvious physiological process continuing in the cut forage is respiration and there are always losses of dry matter associated with it. Wiegner (1925) put the figure at a varying level witb a maximum of around 10 per cent, but does not differentiate hetween respiration proper and other hiological processes.

It should be realized that during the early stages photosynthesis may continue and with it there will be assimilation and in hright sunlight this may actually result in a dry-matter gain. Fleischmann (1912) has shown such gains during the earliest stages of drying and other workers (Nash, 1956) have confirmed this fact. These gains, however, are gradually overshadowed by the losses due to respiration and other destructive hiological processes as the cut herhage loses the capacity for photosynthesis hecause of the 'death' of the cells. It is thus evident that there must be some loss of value in the crop after cutting and this

will vary with the speed of the drying process. Bosch and Deijs (1950) put the loss of dry matter during partial drying after cutting at 2·5–3·0 per cent for each 24 hours. This is a matter that will have to be considered more fully later when discussing the wilting of crops in the field as a preliminary to one or other of the conservation processes. The need for such a reduction in moisture content may best be seen in artificial drying. The main economic problem is the cost of evaporating water, so that it is advisable to reduce the moisture content to the lowest level compatible with retaining as much of the dry matter without breakdown or loss as is possible. Disregarding the small loss of dry matter that may take place during field wilting it is obvious that the process will cheapen costs and is frequently adopted by operators of grass dryers. If, for example, a sample originally containing 80 per cent of moisture is allowed to wilt to 60 per cent, then 80 lb. of water would have to be evaporated to produce 20 lb. of dry matter in the fresh crop, whereas in the wilted crop it will only be necessary to evaporate 60 lb. of water and the output of dry matter will be doubled since the wilted herbage contains 40 per cent.

Most conservation processes commence with a period during which the crop lies undisturbed in the field and changes in the chemical composition may be much greater than is generally imagined, but before the exact changes and their magnitude can be measured a great deal of work still remains to be done.

ARTIFICIAL DRYING

The changes that occur during the actual process of dehydration must be separated from those taking place in the field which have already been discussed. This is necessary because a large number of drying plants as a matter of commercial practice allow the crop to wilt before it is brought to the actual dryer. Normally the crop is not allowed to wilt for a very long period so that the changes are not so marked as in the case of natural drying to be considered later in this chapter when dealing with hay. There are many types of artificial dryer in common use and the chief difference that exists between them is the length of time involved in the removal of moisture. This in turn will depend upon the actual temperature of the drying gas, heated air, and this may range from as low a value as 80° C. to as much as 600° C. and over, the actual speed of drying varying from 20 minutes or so to as many seconds.

Under conditions of proper management all these dryers give a

product of similar value as is shown by the following table based on a large number of samples examined by the author (Watson, 1949) The digestibility of the crude protein fraction of the sample is taken as an index since this is the factor that is most easily affected The samples were not strictly comparable but all the values for the digestibility of

TABLE 6 1 *Digestibility of crude protein of samples of grass dried at different temperatures* (Watson, 1939)

Inlet temperature of drying gas ° C	Digestibility of crude protein
80	77 8
140	76 7
250	72 8
350	78 6
600	81 9

the protein are high and a product of this order of digestibility would have a value for the protein similar to that of the fresh crop The digestibility of the dry matter of a dried grass is normally less affected by heat than that of the protein so it could be assumed that the digestible nutrients in the samples tabulated above would be high and comparable to that in the fresh crop prior to drying This can be seen from the next table in which the analyses and digestibility coefficients of two samples of grass are compared with the artificially dried product obtained from them These are from work carried out by the present author some years ago (Watson, 1949) As a matter of interest the table includes some data obtained by Honcamp (1915) who dried some grass in a vacuum dryer in which the temperature never rose above 70° C—ideal conditions for preventing losses or change in general composition Later work has only served to confirm the findings that are summarized in Table 6 2

If the individual groups of constituents are examined it will be found that with one exception the changes are negligible The ether extract values in the fresh crop and dry product show a reasonable agreement The digestibility of this fraction shows no change in one case, a rise in the second and a decrease in the third. Little importance can be accorded to these differences because of the difficulty of getting reasonable values for this constituent, which is normally present in small amounts, making the measurement of its digestibility difficult, especially

TABLE 6.2. *The composition and digestibility of fresh and artificially dried grass* (Watson, 1949)

	Watson								Honcamp			
	Low protein grass				High protein grass							
	Fresh		Artificially dried		Fresh		Artificially dried		Fresh		Artificially dried	
	Comp. % of dry matter	Digest. %	Comp. % of dry matter	Digest. %	Comp. % of dry matter	Digest. %	Comp. % of dry matter	Digest. %	Comp. % of dry matter	Digest %	Comp. % of dry matter	Digest. %
Ether extract	2·11	55 9	2·40	55·4	2·09	38·9	2·79	53·1	3·58	94·6	3·43	61·6
Crude fibre	30·43	70·3	28·20	72·3	21·95	80·4	21·92	78·1	30·75	67·5	30·30	68·6
Crude protein	10 62	63·1	10 86	56·1	17·58	77·6	17·83	72·6	15·75	76·2	14·91	73·7
N-free extractives	47·55	69 6	49·27	70 6	44·86	77·5	45·92	77·0	40·75	63·0	42·76	66·5
Organic matter	90·71	69 0	90·73	69·1	86·48	77·3	88·46	75·7	90·83	66·8	91·40	68·3
'True' protein	7·58	55 6	10·08	58·4	13·13	70·8	16 90	72·2	11·51	—	11·66	—
Dry matter	21·10	66 6	90·30	67·3	17·21	74·4	86·42	72·3	17·80	64·1	—	65·3

since it is a fraction that contains many substances other than the true fat

The crude fibre, a fraction based on an empirical method of analysis, shows good agreement throughout both for amount present in the dry matter of the fresh and dried crop and for its digestibility

The same is true of the crude protein though it will be noted that there is a tendency for a slight depression in its digestibility This, however, is small and its significance not great, though the trend is there The nitrogen-free extractives, like the other carbohydrates present in the crude fibre fraction, show good agreement throughout both as regards the amounts in the dry matter and their digestibility Together these two groups constitute the major part of the organic matter and also dry matter of the sample and this is reflected in the values for organic and dry matter which show little change in amount or in digestibility as a result of dehydration The most interesting figure is that for the so-called 'true' protein—the complex of nitrogenous compounds that can be precipitated by copper salts, differentiating these compounds from the simpler compounds present such as amides, ammonium compounds or the like There is evidence here of some change in the crude protein fraction, the amount of copper-precipitable nitrogen rising as a result of the dehydration process It is of interest to note, however, that the larger amount of this fraction present in the dried product is still as digestible as that found in the fresh grass Honcamp using a vacuum dryer which would give ideal conditions does not seem to have obtained evidence of this denaturing of the protein fraction, but no figures are available from his work to show whether or not there was any change in the digestibility of this particular constituent In this connection Morris, Wright and Fowler (1936) determined the biological value of the protein in artificially dried grass and compared it with the fresh grass and found that it was unaffected by the dehydration process It would seem, therefore, that the denaturing that takes place in the protein fraction does not affect its feeding value at least so far as cattle are concerned

The amounts of ash or mineral matter in the fresh grass and the dried grass are very similar as can be seen by comparing the values for organic matter, since the difference between these and 100 will represent the mineral matter It is not possible to go any further than this since there is no way of measuring any change in the form of the different elements in the mineral-matter fraction As a general statement it can be said that the dehydration does not appear to have affected the mineral matter

The fate of the vitamins is also of importance and it will be expected that ascorbic acid (vitamin C) will be lost during the process since it is readily destroyed by heat. Carotene as precursor of vitamin A is a valuable constituent of green crops and is retained during artificial drying to a remarkable extent as will be seen when considering the losses inherent in the process; it is during storage of the dried product that the greatest losses of carotene take place as a result of oxidation.

It has been assumed so far that the drying process has been properly carried out and this is true of most commercial dryers which are so adjusted that the heat is used to evaporate moisture and is not allowed to raise the temperature of the final product unduly. The danger of loss of digestibility and also of carotene arises if the dried grass is not removed as soon as it is dried from the sphere of action of the hot drying gases. Normally the grass coming from a dryer is warm to the touch but never very hot. That some overheating may take place is evident in certain types of dryer where portions of the sample have lost their fresh green colour and have a brownish tinge and a caramelized-sugar smell.

In an experiment carried out by the author in 1933 at Jealott's Hill, grass was exposed to hot air at three different temperatures for varying periods up to an hour and samples were taken at intervals for examination. The digestibility of the protein was measured in the laboratory by *in vitro* methods and the carotene content of the material was examined. It took about five minutes to dry the material thoroughly and after this the figures represent the exposure of *dried grass* to different temperatures. The following figures show that the digestibility of the protein and the carotene content both fell with length of exposure of the dried grass to hot air.

The results of this experiment are conclusive and show the danger of exposure of dried grass to hot air. In practice high outlet temperatures of the air in a dryer may cause trouble. Hodgson *et al.* (1935) in an experiment with differing outlet temperatures showed that it was only when the outgoing gases rose to 205° C. that any marked depression of digestibility or large loss of carotene was noted. The actual losses that arise during the dehydration process are lower than in any other method of conservation, but the volume of data on losses is not great and it is too freely assumed that they are negligible. Barr (1933) in Louisiana found it impossible to make a proper balance-sheet and suggests that there is always a mechanical loss due to fine particles escaping with the exhaust gases. A cursory examination of any

TABLE 6.3 *The effect of exposure of dried grass to hot air at three different temperatures* (Watson, 1948)

Temperature °C	Time of exposure min	Digestibility of protein %	Carotene Mg per 10 gm
160	10	82·9	25 1
	60	46 4	4·7
180	10	83 4	16 8
	60	27 8	2·0
200	10	41 3	7 7
	60	9 9	0

commercial plant will show this to be true and it makes the determination of actual losses due to dehydration difficult to measure unless the large volumes of exhaust air can be passed through filters

In an early experiment at Jealott's Hill (Watson, 1949) there was a complete recovery of the dry matter in two samples of dried grass that were made in a band dryer, removing the product while it still carried about 25 per cent of moisture and was thus not so likely to be carried away in the exhaust gases In a third test where the moisture was reduced to under 10 per cent which is more comparable to commercial practice the loss of dry matter was 3 3 per cent In a further trial three replications the loss of dry matter was 8 1 per cent and the losses of the individual constituents was also of this order throughout The experiment was repeated the next year with losses in dry matter varying from 6 9 to 12 0 per cent

American data from Vermont (Camburn *et al*, 1942) show losses of dry matter varying from 2 8 to 6 9 per cent, using grass and also lucerne Swedish results quoted by Edin *et al* (1931) with different crops show losses of the organic matter of 5 per cent in two cases and only 1 per cent in the third In two of the trials the material, dried in a rotary drum dryer, was overheated and the losses of digestible protein were extremely high The losses in energy value, stated as starch equivalent were found to vary from 9 per cent in the case of satisfactory drying to as much as 20 per cent where the crop was overheated Koeniger and Hammer (1931) in Germany obtained figures for dry-matter losses of the order of 8 per cent varying from 0 1 to 36 3 per cent and if this last value is ignored the losses averaged just under 1 5 per cent Other data show variations very similar to the figures

already quoted and it may be assumed that in practice the loss of dry matter during artificial drying will be of the order of 5 per cent, the loss falling more or less equally on all the constituents, much of it probably being of the nature of a mechanical loss. The dried product may similarly be assumed to have a mineral composition more or less identical with that of the original fresh crop. In short the process is almost entirely a matter of dehydration, composition and digestibility of the dry matter in the crop remaining unchanged in the average dryer under good management.

Turning to the vitamins, one would expect a more or less complete loss of vitamin C and green crops in general are not good sources of vitamin D. Scheunert and Schieblich (1934) found that the vitamin-B complex was unaffected during the drying process as might indeed have been expected. They also found a high carotene content in artificially dried grass as compared with field-dried grass in which it was almost completely destroyed.

Experiments at Jealott's Hill (Watson, 1949) showed a high recovery of carotene as may be seen in the following table.

TABLE 6.4. *Carotene content of grassland herbage before and after drying* (Watson, 1939)

Date	Carotene as mg. per 100 gm. of dry matter		Percentage recovery
	Fresh grass	Artificially dried grass	
29.10 1931	42·2	40·4	95·7
3.11.1931	48·4	43·9	90·7
11.11.1931	56·2	47·5	84·3

There is a further loss that has to be taken into account in the case of ıe carotene in dried grass, because during the storage of the dried grass ıere is a constant and progressive loss of carotene due to oxidation. :onditions that allow of ready access of air and light will result in rapid estruction of the carotenoid pigments. Waite and Sastry (1949) ummarize the position by saying that the loss of carotene in a dryer ıeed not exceed 10 per cent but there can be a further loss of 30–40 per :ent as a result of storage for six months. Since much of the value of łried grass rests upon its carotene content, the conditions of storage are important. Fortunately, as the carotene is lost by oxidation, so too are the chlorophylline pigments destroyed and the green colour of the

sample may be used as a visual guide to the degree of exposure to oxidation the sample has suffered and thus to the loss of carotene

Another possible source of loss that is often overlooked is the effect of the dehydration process on the energy value of the product and this calls for work on the measurement of the true net energy value of all grassland products In the calculation of the starch equivalent value of animal foodstuffs from the digestible nutrients a correction has to be made for the total crude fibre present and this has normally been based on the factors given by Kellner (1915) A succulent fodder with its low fibre content calls for a deduction of 0 29 lb of starch equivalent for every unit per cent of crude fibre in the crop so long as it does not exceed 4 0 per cent The deduction factor rises regularly to a value of 0 58 lb of starch equivalent when the crude fibre content in the food is 16 per cent or more Fresh grass containing 4 per cent of crude fibre may in a matter of seconds be transformed into dried grass with 18 per cent The deduction would be 0 29 lb starch equivalent in the fresh grass and the question arises as to whether or not it should remain at this level in the dried product or whether it should be increased to 0 58 With 18 per cent of crude protein this means the difference between a reduction of 5 2 and 10 4 lb of starch equivalent or about 8 per cent of the total starch equivalent content of the sample If the higher deduction is the correct one then artificial drying carries with it a further loss of 8 per cent of nutritive value In the absence of accurate information different workers have applied one or other of the possible deductions or have taken a midway course (Dijkstra 1954) Woodman and Eden (1935) in calculating the feeding value of artificially dried lucerne meal have used the value 0 29 but Crasemann (1954) has queried the use of the two extremes and found there was 16 per cent loss in net energy value and favours an intermediate correction factor Until definite values have been determined it might be better to give the product the benefit of the doubt and this has been done in the present chapter

The feeding value of dried grass and incidentally that of all conserved products dealt with in this chapter varies with the class of stock to which it is fed and normally it may be said that it is most suitable for ruminants and the horse all of which are capable of dealing with the fibrous nature of these materials For simple stomached animals such as the pig and poultry they are not suitable sources of energy or protein but they may however be used as vitamin supplements their value depending largely upon the carotene they contain The market

value of dried grass depends to a considerable extent upon this special virtue and large amounts are used as constituents of mixtures for such stock, the samples being valued on the basis of carotene content. At one time this led to considerable difficulties in evaluation since dried grass was graded entirely upon its carotene content and the margin allowed for storage losses was such that a high-grade sample might have a low energy and protein value. Such samples gave disappointing results where it was thought that a high-grade dried grass would be a good source of protein and starch equivalent. Nowadays the material is included in the schedules of the Fertilizer and Feeding Stuffs Act and a truer evaluation is possible.

TABLE 6.5. *Grading of artificially dried crops*

Dried grass	Any product which (*a*) is obtained by artificially drying any of the following: grass, clover, lucerne, sainfoin, green cereals or any mixture consisting of any of these and (*b*) is otherwise as grown (that is to say including any growths harvested therewith but with no other substance added thereto) and contains not less than 13 per cent albuminoids (protein) calculated on the assumption that it contains 10 per cent moisture.
Dried grass (maintenance quality)	Dried grass as defined in the schedule except that it may contain less than 13 per cent, but not less than 10 per cent albuminoids (protein) calculated on the assumption that it contains 10 per cent moisture.
Dried green fodder crop	Any product which (*a*) is obtained by artificially drying any green crop or crop suitable for use as dried fodder for cattle and poultry and (*b*) is otherwise as grown (that is to say including any growths harvested therewith but with no other substances added thereto) and contains not less than 10 per cent albuminoids (protein) calculated on the assumption that it contains 10 per cent moisture, but is not dried grass or dried grass (maintenance quality).
Dried green roughage	Any product which contains less than 10 per cent albuminoids (protein) calculated on the assumption that it contains 10 per cent moisture but which in all other respects complies with the definition of dried grass or dried green fodder crops.

Watson (1948) has suggested a simple classification of dried grassland products based on a knowledge of the stage of growth and relative leafiness of the original material. In the absence of this knowledge a

chemical analysis is essential and as a general rule, with artificially dried crops the crude protein content is a sufficiently good guide to the evaluation of the feeding value of the sample.

TABLE 6 6 *Nutritive value of artificially dried crops* (Watson, 1948)

	Dry-matter content %	Crude protein %	Per 100 lb Starch equivalent lb	Protein equivalent lb
Grass Very leafy	90	18 7	54 1	13 6
,, Leafy	90	15 0	51 7	9 3
,, Little stem early flowering stage	90	12 1	51 2	6 8
,, Stemmy, flowering stage	90	10 4	49 5	5 5
Lucerne or clover bud stage	90	22 3	50 1	13 6
Lucerne or clover, early flowering stage	90	16 2	44 1	10 5

The protein is stated in terms of protein equivalent which is the average of the values for digestible crude protein and digestible true protein Values cannot be quoted for mineral matter and carotene, but as a general rule the higher the protein the better the sample will be as a source of both minerals and vitamins, subject of course in the latter case to age and conditions of storage

NATURAL DRYING

The normal method of conservation in agricultural practice is still that of haymaking in which natural drying is employed The changes that take place are a continuation of those that have already been noted but they proceed until the death of the cell The crop is subjected to prolonged enzymic action and to considerable changes due to respiration, all of which take a fairly heavy toll of the plant constituents and particularly the carbohydrates in the crop The extent of these changes will depend upon the length of time taken by the crop to reach the stage at which they are stopped by the death of the cells Crasemann (1925) put the losses falling on the carbohydrates at 69 per cent, affecting mostly the digestible portion of this fraction, and assesses the loss of crude protein at 15 per cent

The weather at the time of haymaking may also have a marked effect and rain is a potential source of loss of soluble material which may be leached out of the dried hay, though it will not be able to do much damage in the early stages of drying while the cells retain a degree of impermeability. A succession of light showers may leach out more nutrients than does heavy rain.

After the crop is dried there may be mechanical losses due to the separation of the brittle leaves which dry out more rapidly and are liable to shatter easily. Since the leaf is always richer in nutrients than the stem, this loss will be heavier than the figures for dry matter alone suggest. Ames and Boltz (1912) put the loss of leaf under favourable conditions as high as 15 per cent of the weight of lucerne hay and Gerlach (1929) quotes figures up to 35 per cent in the case of leguminous crops and 5 per cent with grass. Care is thus essential in haymaking and modern mechanization may bring about heavy losses.

After the hay is carted from the field it still has a fairly high moisture content and is capable of fermentation in the stack and this will result in further losses again largely falling on the carbohydrates in the crop.

Wiegner (1925) has summarized the losses that take place in haymaking under good conditions and the losses are considerable.

TABLE 6.7. *Losses occurring in haymaking in good weather* (Wiegner, 1925)

	Dry matter %	Digestible dry matter %	Starch equivalent %
Respiration	up to 10	5–15	5–15
Mechanical losses	5–10	5–10	5–10
Fermentation in the stack	5–10	5–10	5–10
Increased energy needed for digestion			10–15
Total	10–30	15–35	25–50

It should be noted that the loss of digestible carbohydrates and the increase in the crude-fibre content consequent on the process, increase the need for energy in digesting the hay as compared with the original fresh grass and this is reflected in the losses of starch equivalent. This emphasizes the need for fuller information on the energy value of hay and shows that the loss of dry matter is a misleading figure, lower always

than the actual loss in feeding value The figures in Table 6 7 are representative of Swiss practice but are very similar to those that have been obtained in the British Isles The figures in Table 6 8 were obtained over a series of years at Jealott s Hill and include all losses in the field and in the stack.

TABLE 6 8 *Summary of losses in haymaking 1932–5 Stated as percentages* (Watson 1951)

	Weather conditions	Dry matter	Crude protein	Starch equivalent	Protein equivalent
Early-cut hay					
1932	Good	25 5	18 0	45 1	44 1
1933	Good	21 0	16 5	38 5	29 2
1934	Very dry	10 0	2 4	23 0	8 9
1935	Showery	36 5	29 2	58 7	45 9
Average		23 2	16 5	41 3	32·0
Ordinary hay					
1932	Showery	36 7	41 5	48 4	53 7
1933	Good	17 4	14 6	33 0	28 7
1934	Very dry	10 4	4 5	23 0	17·0
1935	Good	15 6	24 4	23 5	18 1
Average		20 0	21 2	32 0	29 4

The figures illustrate most of the points that have been made above The early-cut hay was made some three weeks before the ordinary hay in order to obtain any advantage that was possible due to better composition It was found that the yield of dry matter at the early date was about 60 per cent of that of the ordinary hay and it was in general more difficult to make the hay well at this stage This shows up in a greater loss of both starch equivalent and protein equivalent more especially of the former The effect of wet weather is clearly seen and affects both the energy value and the protein In 1934, which was a very dry year the losses were low but even here there was a loss of nearly 25 per cent of the energy in the original crop, though the protein losses were low In these experiments fairly large plots were used so that machinery could be employed, thus ensuring some of the normal mechanical losses in the field. The hay was taken to the stack when it was fairly dry so that no excessive fermentation took place

The figures show that on the average one-third of the nutrients in the crop are lost during haymaking and the figure may easily go up to half, whilst under really bad conditions the loss may be even more serious. Hay as it goes to the stack still has the power to ferment and it is possible for overheating to take place causing a considerable loss of digestibility, especially of the protein. In extreme cases the hay is badly charred and sometimes fires break out in overheated stacks.

Geering (1939) has reported on Swiss results and his figures are typical of what may occur (see Table 6.9).

TABLE 6.9. *The effect of overheating in the stack* (Geering, 1939)

	Temperature °C.	Colour	Smell	Increased percentage losses	
				Starch equivalent	Digestible protein
Normal fermentation	Up to about 50	Normal	Normal	—	—
Marked fermentation	50–60	Dark	Slightly aromatic	5–10	10–30
Excessive fermentation	60–70	Brown	Sharp aromatic	10–30	30–80
Overheating	over 75	Black	Burnt	30–60	80–100

Similar data are quoted by Bechtel *et al.* (1945) for normal hay, brown hay and black hay. The digestibility of the dry matter was 60, 41 and 27 for the normal, brown and black hays respectively whilst the protein values were 67, 16 and 3 per cent for the respective hays. From these figures it is obvious that the feeding value of overheated hay will be low, that the results in practice will fall far below the levels that might be suggested by the chemical composition of the samples, and that full allowance must be made for this serious fall in true feeding value.

Despite the marked changes that take place in haymaking the composition of the product does not differ markedly from that of the original crop if care is taken. It is really the stage of growth at which the hay crop has to be cut that determines its feeding value. It is always relatively mature at the time of year when conditions are suitable for haymaking and so is inevitably a bulky, fibrous foodstuff

with a low protein value. The tendency in practice is to allow the crop to become very mature before cutting in order to get the greatest bulk of hay and at this time it is easier to 'win'. Most of the hay made in the British Isles is cut at such an advanced stage that the plants have flowered, have finished their normal life cycle and are at the lowest point as regards both their protein composition and their digestibility.

A comparison of the analytical values for the ordinary hays made at Jealott's Hill and summarized in an earlier table is given below.

TABLE 6.10 *Composition and digestibility of fresh grass and hay made from it**
(Watson, 1949)

	Grass		Hay	
	Composition % dry matter	Digestibility %	Composition % dry matter	Digestibility %
Ether extract	2·31	53·8	9·93	40·9
Crude fibre	28·32	63·8	29·63	66·9
Crude protein	8·15	54·8	8·04	46·8
N free extractives	53·95	72·5	52·99	67·0
Ash	7·27	—	7·41	—
'True' protein	6·89	50·5	7·00	43·9
Dry matter	30·8	66·5	86·5	63·2

* Average of four years 1932–5

composition and digestibility might well be less favourable than appears from an examination of the figures for well-made meadow hays.

It is important to consider also the effect on the mineral constituents, though there is very little information on this point. The crop when cut usually has a low mineral content and there may be a loss due to the mechanical shattering of the leafy portions that are particularly rich in this constituent. Crasemann (1934) has reported losses of the order of 7 per cent under normal conditions rising to as much as 35 per cent with rainy weather.

The position with regard to the vitamins in hay has been summarized by Watson (1951) and shows that on the whole, hay is a poor source. There is always a marked destruction of vitamin C, and in rainy weather up to half of the vitamin-B complex can be leached out, though normally little loss occurs. It is claimed that the solar irradiation that hay undergoes may increase its content of vitamin D. There is evidence for this with lucerne hays in America, but it should be realized that hay, even if subjected to solar action, can never be a good source of this vitamin since the precursor is only present in small amounts.

The most obvious change in haymaking is the bleaching and loss of colour that takes place. During the process most of the carotene is lost so that the vitamin-A potency of hay is normally very low, though it may be retained to some slight degree by modifications in the hay-making process. Hodgson *et al.* (1948) comparing the making of lucerne into hay in the field with a drying process to complete the field curing, obtained the following values which may be regarded as typical

TABLE 6.11. *Changes in carotene content of lucerne hay as compared with fresh crop* (Hodgson *et al.*, 1948)

Time sample was taken	Carotene content in dry matter: Cured in field μ gm. per gm.	Finished in dryer μ gm. per gm.
When cut	297	308
When put on dryer	—	122
When dry (after 13 days)	—	29
When stored	49	—
When stored for 30 days	26	—
When fed	12	22

of haymaking conditions (Table 6 11) The fall in carotene content is very marked and reaches an almost negligible value when it is finally fed to the animal The additional drying process, to be described later, has helped to some extent, but even here the final product, though double the potency of the field-cured material, is only a mere shadow of the original crop

The figures are self-explanatory and it will be seen that the loss is mainly in the field though even after that the losses continue until the hay finally reaches the animal Many efforts have been made to reduce the magnitude of the changes in the field Acceleration of the drying process is of paramount importance and practical control of the field work may affect the results that are obtained, but these lie outside the scope of this work. The crushing of the crop in order to speed up drying was first developed in America and has been of value there since most of the hay is made from lucerne in which there is a thick stem that dries slowly and a leaf that will dry quickly The crushing of the stem evens the rate of drying of the two physical components of the crop and thereby reduces mechanical loss In this country crushing or bruising (Nash, 1956) has had no marked effect on speed of drying, except in the uppermost layers of the swathe where bruised material dried at a faster rate than the mown crop

For many years, particularly in northern Europe, special appliances to reduce the hazards in haymaking have been in general use These vary from stakes driven into the ground on which the partially made hay is hung, in the simplest case, to wire-strand fences erected in the field on which the hay is carefully built, layer by layer Tripods and hurdles are the intermediate form of hay-making appliances In all these cases the hay is allowed to dry out partially on the ground and long before it would be fit to put in a stack it is built on to the appliance The result of this is to prevent most of the mechanical loss since the crop is not dry enough to shatter In addition it is always carefully built on the appliances and thus will shed rain readily in the later stages of drying when it is most liable to heavy losses by leaching, which is not possible with the freshly cut crop where the cells still retain their faculty of preventing the free passage of their contents Also the crop does not lie for so long freely exposed to oxidation and light and therefore the green colour is retained to a greater degree as is also some of the carotene

Swiss data of Landis *et al* (1932) summarized extensive trials of different types of appliances These show an advantage of the order

TABLE 6.12. *Losses in hay made on the ground and with special appliances* (Landis *et al.*, 1932)

	No. of comparisons	Dry matter %	Digestible protein %	Starch equivalent %
All weathers				
Dried on the ground	79	20·9	32·9	41·6
Dried on special appliances	79	17·2	27·6	37·2
Wet weather				
Dried on the ground	41	25·7	39·5	45·4
Dried on special appliances	41	20·8	31·8	39·2

of 7 per cent in nutritive value due to the use of these appliances in bad weather, and of approximately 5 per cent in normal weather. In a really bad year, however, they might make all the difference between getting a crop and losing it. The actual changes in the hay itself would not be expected to be very different from those in hay made on the ground apart from a certain amount of saving in the loss of carotene due to protection from direct sunlight.

In Britain the use of special large heaps of hay, sometimes built round a tripod, is common in the more northerly parts where weather is less favourable to rapid drying. The use also of special tripods that allow access of air to the centre of the heap is becoming common. It will give a hay of better colour with a slightly greater vitamin-A potency, but the reduction of actual field losses cannot be expected to be greater than that already indicated for mid-European conditions. In modern haymaking practice, however, mechanization is so great that mechanical losses must be high so that the use of the tripod might well have a beneficial action in counteracting the increased losses that must follow heavy mechanization.

Baling of hay in the field will mean that the chances of mechanical loss are again lessened, but the general picture must be similar to that under normal conditions of haymaking and the main advantage accruing will be due to a more economical use of labour. In the case of baling there is a counter-factor in that the crop must be baled when the moisture is at a sufficiently low level, often put at 25 per cent. Otherwise it may heat severely in the bale which may later mould or

may even give rise to conditions similar to those that arise in the 'spontaneous' combustion of haystacks with the usual harmful overheating of the hay or complete loss

There has been a rediscovery of the possibility of finishing off the field-curing of hay by blowing cold air through the partially made hay in layers of suitable depth, a process tested long ago in this country and discarded. The American workers claim an advantage for the process, but under our conditions, the humidity is normally too high at those periods when the simple dryer envisaged is most needed The drying agent is the heat resultant on fermentation and this is blown through the mass to dry it out It will be obvious that such a process will result in a loss of carbohydrates and the extent of this change must be balanced against the practical advantages The trend with these barn dryers, as they are called, is to turn the use of heated air so that in effect it has now become a question of artificial dehydration The changes and the losses will, therefore, be a reflection of what happened in the field and during transit to the dryer since, if it is properly operated, the dryer should check quickly all subsequent changes and there should be no further loss in nutritive value It should be noted that the carotene content suffers heavily as will be seen from Table 6 11 when it was reduced to one-third in the field and to a tenth during the barn-finishing process

TABLE 6.13. *Nutritive value of hay* (Watson, 1948)

	Dry-matter content %	Crude protein %	Per 100 lb. Starch equiv. lb.	Protein equiv. lb.
Meadow hay:				
early flowering stage	85	10·0	40·5	5·0
flowering stage	85	7·6	35·6	3·1
full flower, seed set	85	4·8	32·5	2·0
Seeds hay:				
high clover	85	12·2	45·0	7·0
medium clover	85	9·1	42·8	4·5
low clover	85	7·4	44·3	3·5
Lucerne hay:				
before flowering	85	16·4	32·2	10·2
full flower	85	14·5	27·1	8·1

roughages, though this does not mean that hay is not a most valuable foodstuff.

ENSILAGE

In the ensilage process the crop is conserved whilst the moisture content is at a relatively high level, and the process depends upon the control of certain biological changes if the product, silage, is to be satisfactory. Unlike haymaking it is independent of the weather and this means that full advantage can be taken of the higher nutritive value of young, leafy green crops: it resembles artificial drying in this respect. As a result, silage should never be compared with hay; they are products of a complementary nature and in no way competitive. Indeed at the stage at which hay has normally to be made in Britain the crop is at such an advanced stage of growth that it is difficult to ensile, and it is usually preferable to make hay of it if drying conditions are suitable. If a crop has reached the hay stage it should be ensiled only as an emergency method, realizing that the product will be of low nutritive value.

When the crop is cut for silage it will continue to respire, the enzymes will still be active. The changes that are associated with these biological processes have already been considered earlier in this chapter. When the cut herbage is put into a heap there will be a certain amount of air entangled in it and aerobic respiration will continue until this is used up. The temperature of the mass will rise and this is an indication

of the degree of respiration that has taken place Undue aerobic respiration will result in a marked reduction in the amount of carbohydrates in the crop with consequent losses in nutritive value Excessive temperature, as in hay, will also result in a diminution in the digestibility of the constituents, particularly the protein This was shown clearly by Woodman and Hanley (1926) working with a stack made from a mixture of grass and clover The digestibility of the dry matter was 47 2 per cent, of the organic matter 49 3 per cent and of the crude protein 12 2 per cent That this was due largely to the difficulty of excluding air may be seen from results obtained by Watson (1951) in which a stack of silage was made in the usual way and compared with one in which the grass was ensiled in a simple movable container This enabled the amount of air to be controlled during the early stages and after some days when the silage had settled to its final compact stage, the casing was removed and later the digestibility was measured

TABLE 6 14 *Composition and digestibility of a sample of stack silage and of a sample of silage made from grass in a movable casing*

	Stack silage		Silage made in movable casing	
	Dry matter %	Digestibility %	Dry matter %	Digestibility %
Ether extract	2 9	57	4 1	66
Crude fibre	31 3	84	26 4	70
Crude protein	18 9	42	18 4	68
Nitrogen free extractives	32 5	49	40 2	67
'True' protein	15 3	30	12 4	52
Starch equivalent	40 6	—	49 2	—
Protein equivalent	6 7	—	9 5	—

The effect of controlling the air in the mass is obvious and shows up in the reduction of starch equivalent value and even more so in the case of the protein equivalent. It should be noted that the ordinary stack was very carefully made and the depression of digestibility was reduced to a considerable degree Had it been as marked as in the case investigated by Woodman and Hanley (1926) the difference in nutritive value would have been still more evident

Associated with high temperatures in ensilage there is always a marked colour change, the resultant silage always being of a dark-brown colour with a sweet smell, from which it has usually been called 'sweet' silage. This type of silage must be guarded against at all costs and usually results when the temperature of the mass reaches 120° F. and over.

The early history of ensilage in Great Britain followed on the successful exploitation of the process in France as typified by the work of Goffart (1877) who used a pit in which the mass reached a relatively low temperature. This was modified by Fry (1885) who advocated cutting the crop at an advanced stage of growth and allowing it to reach a temperature of 125° F. and over to produce a sweet silage, a policy that set back silage here for fifty years.

It is clear that the first principle in ensilage is to restrict the amount of air in the mass so as to reduce aerobic respiration to the lowest possible level. Even when this has ceased it must be remembered that anaerobic respiration will continue for some time until the cells 'die' and enzymic changes also stop.

In practice it means that some sort of container should be used to control the access of air. Many different containers, or silos as they are called, may be used. In some countries the tower silo is in general use, in others the pit or trench silo is more popular, but in all these free access of air is prevented. The use of overground trenches with walls made of some suitable material—concrete, wood, or even closely packed bales of straw—has become popular and here again the amount of air is under control. Silage made in high stacks or in low heaps, that are properly called clamps, though often weigbed down with a layer of soil, still have sides open to the air and the resultant silage will always suffer as a result.

In Great Britain the crop is often ensiled in an unchopped state and it calls for careful filling to prevent pockets of air that will result in local overheating, often followed by mould. Where the crop can be chopped it will pack more closely and control of air is much simpler.

It is necessary to compress the mass in the silo as thoroughly as is possible during filling and it should be sealed off from the air when the silo is full. A layer of soil is best for this purpose; it acts as an air seal and also continues to exert pressure on the mass, preventing the later access of air. Finally it is advisable to put a cover of some sort over the whole silo to prevent leaching by rain during the storage period. Where this is not done leaching by rain may often start undesirable

fermentations resulting in losses in feeding value and deterioration in the quality of the silage at the top and sides

After the cells have 'died', their contents are freed by the pressure on the mass and the various micro-organisms present on the surface of the herbage begin to act The general result of the micro-biological changes in good silage is to produce lactic acid. If this can reach the requisite concentration it controls the action of less desirable organisms that produce butyric acid, with which is normally associated an extreme breakdown of the protein to ammonium compounds The level of such volatile bases is another indication of bad silage Rapid increase in the acidity of the mass is, therefore, the second requirement of good ensilage This is due to the fact that the lactic-acid forming organisms withstand relatively high concentrations of acid whilst other organisms cannot do so

There are indications in the early literature that the need for rapid acidification was realized, but the final establishment of the underlying principles of acidification and their proper application in practice is due to Virtanen (1933, 1934) who started work on the problem in 1925 He showed that at pH 4 2 the growth of butyric acid and other harmful organisms ceases, that breakdown of protein is almost inhibited below pH 4 0 whilst respiration is rapidly suppressed as acidity rises and at pH 3 5 is only about 20 per cent of the normal, ceasing completely at about pH 3 0 All subsequent work has fully substantiated the importance of the acidity of the mass in producing good silage

These findings gave rise to the A.I.V. process of direct acidification to which reference will be made later.

In well-made silage the final product is very similar to the crop ensiled, both as regards composition and digestibility. This can be seen from a comparison of a number of silages made in towers and in lined pits (Watson, 1949).

The figures for ether extract show an increase because the organic acids appear in this fraction and therefore the two sets of values cannot be compared. The crude-fibre values rise because of diminutions in nitrogen-free extractives and other constituents lost during ensilage and the digestibility coefficients show little change.

The crude protein content appears to have risen, but this again is due to an arithmetic rise because of the loss of nitrogen-free extractives and an overestimation due to the use of the factor of 6·25 in calculating crude protein from total nitrogen values, irrespective of the fact that a larger proportion of the nitrogen is in the form of simpler nitrogen compounds. The protein has not suffered in digestibility to any marked extent.

The 'true' protein shows a marked diminution due to breakdown to simpler nitrogenous compounds, though these are not necessarily ammonium compounds or other volatile bases. The digestibility of this fraction shows a fall since the more readily digestible part will have disappeared first in the course of the breakdown of nitrogenous compounds in the silo.

The nitrogen-free extractives show a considerable reduction, as might be expected, due to losses in respiration and other biological changes during the fermentation process. Here again there is some reduction in the digestibility of the fraction since, as with the 'true' protein, the more digestible part of the nitrogen-free extractives will have been lost first in the changes that take place in ensilage.

On the whole the figures show that the nutritive value of the silage will not differ materially from that of the original crop where conservation has been good. This applies to the silage made under most conditions, the exception being silage that has overheated, which, it must again be emphasized, may have a very low feeding value indeed where the overheating has been excessive. There are some cases noted in the literature in which the protein has been incapable of digestion, despite a reasonable level of crude protein in the silage.

The process of ensilage is based on biological fermentative processes and the difficulty is to ensure that they always proceed in the desired

direction, towards the rapid acidification of the mass Whether or not this will happen depends upon many factors, the chief of which is an adequate amount of fermentable carbohydrate from which lactic acid will be formed This is the reason why maize silage has been such a great success in the United States making silage a foodstuff in common use The maize plant cut at the proper stage of maturity is so rich in sugar that it brings about a rapid formation of lactic acid with relatively small nutritive losses in the crop With most crops as they approach maturity the carbohydrate contents rise and the amounts of fermentable compounds rise too In young crops especially the leguminous crops there is a relative shortage of available carbohydrates and the course of fermentation may frequently lead towards the formation of butyric acid with a marked breakdown of the protein Thus the stage of growth of the crop and its botanical composition must be taken into account if the best results are to be obtained These factors also effect the control of air in the silo, the young leafy crop packing tightly and giving rise to anaerobic conditions with high moisture—conditions most suitable to butyric acid fermentation which must be guarded against in practice As the crop matures and becomes more stemmy, it tends to keep open and aerobic conditions predominate sometimes with excessive heating, unless the crop is thoroughly consolidated

A good deal is written about temperature, and cold-fermentation warm-fermentation and high-temperature fermentation systems are advocated The truth of the matter is that the temperature should be looked upon as the result of the changes in the silo and not their cause Results obtained in a laboratory by heating fresh grass to various temperatures at which they are maintained, bear no reference to field results where the temperatures are an indication of chemical changes that have given rise to heat and that have as a result changed the whole substrate for fermentation, and will have stimulated a totally different chain of biological processes to those in the silage made in the laboratory

The cold fermentation process (Kirsch and Hildebrandt, 1930) which aims at keeping the temperature of the mass below 80° F has developed in the relatively small tower silo filled rapidly, preferably with a chopped crop to which may be added some stimulant. It is sealed off quickly and pressure applied to it immediately, sometimes by the use of mechanical appliances that are exact replicas of those developed in this country in the latter half of last century and discarded since then

It is not applicable to the large tower silo where the excessive pressures in the bottom of the silo may produce anaerobic conditions, with high moistures and resultant butyric-acid formation.

In Great Britain, where the trench silo has developed, it is common to let a certain amount of aerobic fermentation take place in the lower layers, particularly with young succulent crops. Subsequent layers can be filled in as rapidly as is desired. If this practice is not followed the lowest layer is often waterlogged and is high in butyric-acid content. A temperature of about 100° F. is aimed at as this seems to coincide with a fermentation in which lactic acid predominates.

The same end can be achieved by allowing the crop for the first layer to wilt when the fermentation will usually follow a more desirable course than does the very high moisture material. Wilting has been advocated widely in the United States (Shepherd *et al.*, 1948) for dealing with high protein crops and confirmatory evidence is coming from Switzerland (Crasemann and Heinzl, 1949) and the Netherlands (Dijkstra, 1952). The effect of wilting should be to reduce the moisture to between 60 and 70 per cent, though still lower moisture contents have been advocated. The danger with low moistures is that of overheating of the mass in the silos and this is a very real danger in practice.

Nash (1956) has shown that even in what would appear to be unsuitable weather, considerable wilting is possible. It should be noted that silage made from wilted crops does not develop the same degree of acidity as that made from succulent fresh crops; the pH value is higher than would normally be considered desirable, and the biological activity other than respiration is reduced.

The dangers of high temperatures have already been discussed and high-temperature fermentation as a whole is to be deprecated. With protein-rich, leafy crops special precautions have to be taken to ensure a suitable fermentation. The first approach is to stimulate the natural formation of lactic acid by the addition of a suitable carbohydrate. This may best be done by adding a solution of molasses as evenly as possible during the filling of the silo, the quantity used being of the order of 30–40 lb. per ton, though in the United States where lucerne is the normal crop ensiled double that quantity is suggested. It may be worth noting that when the worker in the United States talks of grass silage, he usually refers to lucerne, chopped in a forage harvester and ensiled in a large tower silo. Molasses may be replaced by ground cereals added at the rate of 150–200 lb. per ton. In the Netherlands

finely divided fodder beet or potatoes have been widely used as a source of carbohydrate material in a process often spoken of as the Hardeland process (Dijkstra 1951) though this also includes the use of molasses The basis of the process is a thorough mechanical mixing of the stimulant with the crop

The most rapid means of controlling biological changes is by the A I V process named after its inventor (Virtanen 1933) Here a solution of 2N-strength mineral acid is added to the crop during ensilage in quantities of the order of 13 gallons per ton If evenly added this has the effect of rapidly bringing the whole mass to a pH level of between 3 0 and 4 0 It is the most efficient method of ensilage but in Britain the variation in dry matter of the crop differences in botanical analysis difficulty of handling strong acid on the farm as well as its distribution have all combined to prevent its use It is widely adopted in Scandinavia though the trend there is to replace the mineral acid by an organic acid formic acid has proved cheap and capable of producing similar results in practice to the A I V solution

Many other acids and acid salts have been marketed for ensilage but their action is almost identical with that of A I V solution The difficulty with mineral acids is that some basic material should be added to the silage when it is fed to counteract the effect of the acids added a difficulty that does not arise with the organic acids that are oxidized normally within the animal Virtanen (1933) recommends a mixture of 20 parts of sodium bicarbonate with 80 parts of calcium carbonate to be fed at the rate of 6 25 oz per cwt of silage

The great difficulty in ensilage is to ensure a thorough admixture of the additive whatever it may be and where this is done there seems little difference between any of them Kapelle *et al* (1952) basing the value of the process on the level of the pH value with its associated control of butyric acid and of protein degradation have shown the value of proper mixing of molasses and other carbohydrates with the crop

It will be seen that the percentage of good samples is much greater where thorough admixture of the additive is ensured and it is striking how this shows up With ordinary mixing comparison with the A I V process shows a clear advantage for the latter that disappears entirely where the mixing is good

It is hoped that in the future bruising of the crop in the field may be the answer to this problem If it is done properly a large proportion of cells will be broken down their contents will be evenly distributed

TABLE 6.16. *Influence of hand mixing and mechanical mixing of additives on the quality of the resultant silage* (Kapelle *et al.*, 1952)

	No. of samples	Percentage of samples noted Good	Fair	Bad
Hand mixing of:				
Grass and raw potatoes	58	6·8	6·9	76·3
,, ,, mangolds	217	37·4	27·7	34·9
,, ,, molasses	754	29·7	26·6	45·7
,, ,, A.I.V. solution	208	55·9	17·3	26·8
Mechanical mixing of:				
Grass and raw potatoes	26	30·8	10·2	59·0
,, ,, mangolds	583	62·8	17·5	19·7
,, ,, molasses	97	64·0	28·9	7·1

effluent are not excessive and may be assumed to be of the order of 5 per cent of the original dry matter in the crop

If the silage is well made the losses due to waste at the top and sides should be very low and in most cases negligible

Watson and Nash (1961) has compared the losses of nutrients which are involved when making ordinary, stimulated and acidified silage

TABLE 6 18 *Losses of nutrients involved in ensilage* (Watson and Nash 1961)

Silage	Dry matter		Starch equiv		Digestible crude protein		Digestible 'true' protein	
	Number of tests	Loss %	Number of tests	Loss %	Number of tests	Loss %	Number of tests	Loss %
Ordinary	255	15 9	35	34 3	44	39 8	44	67 4
Stimulated	34	11 7	20	22 9	19	10 0	15	58 1
Acidified	74	12 4	32	23 7	31	10 0	30	40·7

The losses in dry matter need not be high but are misleading, as is seen from a consideration of the losses of energy, stated as starch equivalent The advantage of some additive is noticeable here and is even more marked in the case of the protein There is no separation into growth stages possible, but if it had been, the advantage of stimulation of lactic acid formation or of direct acidification would have shown up even more in the young, leafy, succulent material The losses of 'true' protein are high because of the breakdown to simpler nitrogenous compounds, but a better measure of feeding value of the nitrogenous compounds in silage is the digestible crude protein Somewhat similar results are quoted from Sweden by Jarl (1948) who reports losses of organic matter in 10 samples of A I V silage as 18 9 per cent compared with 19 8 per cent where formic acid was used (27 tests) and 21 1 per cent with the addition of molasses (22 tests) The relative figures for loss of crude protein were 10 7, 11 5 and 8 8 per cent respectively These figures are similar to those in the table and show no modern improvement in treatment with reduced losses

Under American conditions Shepherd *et al* (1948) quote dry matter losses of 10 3 per cent for ordinary grass silage, 8 3 for wilted grass silage, 8 6 per cent where a pH of 4 36 was reached by adding molasses and 5 0 where the pH was lowered to 3 66 by the use of 2N acid solutions Though lower than the European results the relative position of the processes is similar except that there is a definite advantage for direct acidification, which would normally be expected

The losses of energy and of protein in ensilage would appear to be of the order of 25 and 10 per cent respectively. No such data are available for the ash constituents, but in his summary of existing data Watson (1961) states that the losses of ash constituents are not high unless undue leaching with heavy effluent losses has occurred, but even then they do not appear to exceed 10 per cent.

As far as the vitamins in silage are concerned, the losses are not excessive in good samples. Where any degree of heating has taken place, destruction of carotene will be high and a high loss of other vitamins might be expected. The retention of carotene is high and especially so in the A.I.V. process, where the loss is negligible. Shepherd *et al.* (1948) show a loss of 9·3 per cent in such silage rising to 23·5 per cent where molasses was added and 38·3 for silage from wilted grass, where there would be an additional field loss.

The vitamin-C content of silage is reasonable under good conditions of ensilage though half of it may be lost. Silage from a good crop will be a good source of carotene, of the vitamin-B complex and of vitamin C.

The feeding value of silage will depend upon the nature of the crop ensiled and may be a very valuable source of protein and energy, well able to replace concentrated mixtures of oil-cakes and cereals if proper allowance is made for the differing moisture contents.

The silages that are likely to be met in everyday practice can be classified according to the material from which they are made and as the crop retains its structure during ensilage a visual examination of the sample will often allow it to be placed with reasonable accuracy in its proper position as a source of nutrients.

TABLE 6.19. *Nutritive value of silage* (Watson, 1948)

	Dry matter content %	Crude protein %	Starch equivalent lb.	Per 100 lb. Digestible crude protein lb.	Protein equivalent lb.
Grass, leafy high protein	20	3·5	12·4	2·8	2·0
Grass, early flowering stage	25	3·2	14·5	2·1	1·4
Grass, full flower	25	2·9	11·4	1·2	0·9
Lucerne	17	3·7	7·0	2·5	2·0
Clover	20	4·1	8·9	2·7	2·1

To make silage in trenches the following simple rules are suggested and the same principles will apply to silage made in other kinds of container

TABLE 6 17 *Simple rules for ensilage* (Watson, 1951)

Crop	How crop will pack	Method of air control	Is wilting necessary?	Stimulation by use of Molasses	Acid solution*
Short leafy growth (a) Legumes (b) Grasses	Very tightly	Build shallow layers and allow each one to heat to about 100° F	May be an advantage as it will avoid tight packing particularly in a tower silo	Must be used (a) 30–40 lb/ton (b) 20–30 lb/ton	16 gals per ton 13 gals per ton
Early flowering stage some stem	Satisfactory	Lower layers in silo should be allowed to heat. Fill quickly thereafter	Only for bottom layer	Not necessary 10–20 lb/ton may be added as an insurance	13 gals per ton
Full flowering stage stemmy	Loosely	Must be consolidated especially the top layers to prevent overheating	Wilting should be avoided Water may have to be added	Not needed	13 gals per ton

* The solution of mineral acids is of 2N strength

There have been efforts in recent years (Waterson, 1955, Murdoch, 1956) to simplify the handling of silage in the field and these have led to the baling of the fresh crop in modified balers The resultant bales are reported to be easier to handle and are usually of 50–70 lb in weight when made They are packed carefully into the silo, and compressed, often by the use of a heavy caterpillar tractor The advantage claimed is that the bales of made silage are easily separated and when being fed may be lifted out by the strings with which it is usual to tie them It may be said that baling is only a method of handling the crop and has succeeded because, in the main, fairly mature material has been used With young material wilting or the use of some additive is essential and in the latter case metabisulphites have been used with success

Special care is still needed to make good silage and the bales are very liable to heat, even in the field before they are carted to the silo

Careful packing in the silo is essential and consolidation must be carefully and thoroughly done. Many operators use loose grass to fill the spaces between bales and add some between layers and on the top, all of which calls for special care at the silo. No advantage can be expected in regard to quality and yield of finished silage and, unless great care is taken, heating of the mass may take place with all the disadvantages that this entails. Much work still remains to be done before a proper assessment can be made of the process in relation to other methods of handling the crop.

The possibility of excluding air by the application of a surface coat of some kind was suggested many years ago. Modern plastic materials have revived this interest and many plastic sheets have been tested, usually to seal off the surface of the silo. Sprague and Reed (1955) have reviewed current progress and describe a technique of enclosing stack silage in a plastic sheet which is finally gathered at the top and encloses the whole stack. Losses are said to be somewhat lower than in normal ensilage. Experience in this country at present inclines to the view that the plastic materials are too expensive as yet, are not sufficiently strong for the purpose and have too short a life on the average farm.

The ensilage process must of necessity result in some loss of nutrients. The respiration will take toll of the more easily digested portion of the crop and where wilting is practised this loss must be faced, but we have seen that this need not be excessive and need not exceed 3 per cent in 24 hours. In the silo itself the loss due to respiration is not heavy and even where a high temperature develops Woodman and Amos (1926) have shown that this does not involve an excessive loss of nutrients. The fermentation of carbohydrates to lactic acid makes little change in the nutrients since lactic acid has itself a high energy value. The volatile organic acids involve loss, but the end products may be used by the ruminant in due course. Protein breakdown involving simplification of nitrogenous compounds is not so serious in the case of ruminants, to which silage is normally fed and Kirsch and Jantzon (1933) and Watson and Ferguson (1936) have shown that the non-protein nitrogenous constituents of silage can be utilized efficiently by dairy cattle. All these changes go to make up an unavoidable fermentation loss which must be faced in ensilage.

The effluent from silage carries with it dry matter and the loss of nutrients from this cause will vary with the crop and its moisture content as was shown by Sutter (1955). As a rule the losses due to

The values for digestible crude protein have also been included since they are a better measure of the feeding value of silage than the protein equivalent values The grass silages are good sources of energy, whereas the values for the legumes are lower In the latter case both sets of figures relate to silage made from crops cut at the early flowering stage, since they are seldom ensiled at the bud stage because of low yields and difficulties of ensiling material of such a high protein value The silage made from leafy grass on a dry-matter basis is similar in feeding value to the usual concentrated mixtures sold for cattle feeding At the flowering stage grass silage is intermediate between hay and the concentrated mixtures, whilst at the full flower stage it is only equal to hay Normally at this time it is better to let it go for hay.

Stack and clamp silage which normally suffer some degree of overheating should be regarded as equal to full-flower, grass silage even if they have been cut at an earlier stage, since the heating is bound to have reduced the nutritive value

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CHAPTER SEVEN

The Nutritional Physiology of the Adult Ruminant

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The action of saliva: movements of rumen and reticulum in relation to the passage of food—Rumination: chemical changes in the rumen; action of protozoa, bacteria; the digestion of cellulose, fermentation of starch, sugar—Action on protein: digestion and absorption in the rumen, omasum, abomasum and intestines.

Most of the nutritional complications found in the ruminant stem from the fact that fermentative digestion precedes peptic digestion. It is an undoubted advantage for the ruminant to be able to live on a wide variety of herbage and to be able to derive sustenance from coarse fodders that would be of lower nutritional value to a horse and of no value at all to man, but this advantage is gained at the price of a lower efficiency in the utilization of soluble carbohydrates and proteins. All food constituents are subject to microbial digestion in the rumen and the processes involved cause losses of energy and of ammonia nitrogen to occur. It is important to assess the extent to which food constituents are disintegrated before they pass to the abomasum where peptic digestion occurs, to reach a firm conclusion on the significance of fermentative digestion. This involves also the quantitative measurement of soluble products of digestion that are directly absorbed and of the products that pass with the food residues to the abomasum. These measurements present serious technical difficulties that so far have only partially been overcome. It is safe to say that of the cellulose that is digested, 70 per cent or more disappears before the food reaches the abomasum, but it is not possible to be so precise concerning the quantities of organic acids or of the microbial protoplasm that is formed.

The reticulum and rumen together are sometimes said to form a fermentation vat but this is not to say they form an inert vat. These organs are integrated with the whole animal and it is as important to study the activity of the salivary glands, the reflex control of the movements of the stomach the permeability of the epithelium lining these organs their nerve and blood supply and the movements of food through the organs as it is to understand the chemical changes that occur as a result of the metabolism of the bacteria and protozoa that inhabit it

More attention has been given to the rumen than to any other part of the alimentary tract of the ruminant, but from recent work it seems as if the remainder of the tract will prove just as interesting

THE SECRETION OF SALIVA

The saliva of the rumen has three important properties (1) the quantity secreted is unusually large and it provides a continuous flow of water which is important in maintaining the contents of the rumen very moist—the dry-matter content is of the order of 12–16 per cent—and in washing food and other particles that are sufficiently small through the omasal orifice, (2) it has a slightly alkaline reaction containing sufficient bicarbonate to neutralize a considerable part of the organic acids formed during fermentation, it also contains a concentration of inorganic phosphate that is about 5–10 times greater than that of the plasma (3) it contains appreciable quantities of urea and also mucoprotein. Urea is known to be a source of nitrogen that is available to rumen bacteria and mucoprotein is also likely to serve a similar purpose The saliva, therefore, provides a suitably buffered medium containing a small concentration of nitrogen for the culture of organisms in the rumen and its continuous secretion provides sufficient fluid to maintain a continuous flow through the reticulum, rumen and omasum

The principal salivary glands in the sheep have been classified into three groups by Kay (1960) These are as follows group 1, the parotid and inferior molar glands which are serous glands with identical histological appearance, mucous cells can only be found in the major ducts from the glands group 2, the palatine, buccal and pharyngeal glands which are mucus-secreting glands The palatine and buccal glands are small but numerous and are spread over the hard palate and the cheeks respectively, the pharyngeal glands form well-defined masses on the soft palate and at the sides of the pharynx

group 3, the submaxillary, sublingual and labial glands which are mixed glands containing mucous and serous cells.

The serous glands secrete fluids of similar composition which are isotonic with the plasma and well buffered with bicarbonate and phospbate. Both the parotid and inferior molar glands have a slow resting rate of secretion which is independent of the nerve supply and both respond reflexly to mechanical stimulation of the mouth, oesophagus and the reticulum and rumen. The glands of group 2 respond to stimulation in much the same way as the serous glands of group 1. In composition the fluid secreted seems to be similar to that of the serous glands as regards its content of electrolytes but it also contains a high content of mucus. When the saliva from the mouth of anaesthetized sheep is collected after the parotid, submaxillary and sublingual secretions are excluded it is seen to consist of a thick viscous fluid which also has a more liquid component. The volume secreted may be almost as great as the secretions from both parotids and clearly this saliva—named 'residual' saliva by Kay and Phillipson (1959)—is a very important component of tbe total secretion. Residual saliva, however, includes the serous secretion of the inferior molar glands of group 1 and the secretions of the labial glands of group 3.

The submaxillary and sublingual glands both secrete a hypotonic saliva which is weakly buffered. The submaxillary, if it has a resting flow, is very small indeed and is stimulated to secrete mostly by feeding. Little or no responses have been obtained experimentally by stimulation of the oesophagus or of the reticulum and rumen. The sublingual gland, however, has a slow continuous resting rate of secretion and some response may be obtained by stimulation of the oesophagus. Little is known of the flow or responses of saliva from the labial glands.

The fact that the thoracic part of the oesophagus, the cardia and the anterior parts of the rumen and reticulum are the structures that by mechanical stimulation produce a profuse reflex flow of saliva from the glands of group 1 and group 2 suggests that feeding and rumination would be the most potent natural stimulation to salivation (Comline and Titchen, 1957; Ash and Kay, 1959). The parotid gland is known to be stimulated by the two processes in both sheep and cattle, and it is reasonable to suppose that glands that go to form 'residual' saliva as previously defined, behave in the same way as the parotid glands as their reflex responses seem to be the same (Phillipson and Reid, 1958; Kay and Phillipson, 1959).

The flow of saliva in cattle has been measured during eating and

during resting The behaviour of the parotid gland under these conditions and the total flow of saliva in cattle that were neither eating nor ruminating are described by Bailey and Balch (1961*a*, *b*) The interesting feature of the resting rate of secretion of the mixed saliva as it appeared at the cardia was that although eating stimulated the flow the hour immediately after feeding was the period of lowest secretion, thereafter the resting rate of secretion increased until the next meal The electrolyte composition of the resulting mixed saliva in cattle was very similar to that of the parotid glands which is to be expected for under these circumstances the secretions of the sublabial and submaxillary glands are negligible and these secretions are the only ones that differ markedly from those of the parotid as regards electrolyte content

The decreased salivary secretion following feeding may be due to the inhibitory effect of distension of the rumen with food and the subsequent increase in salivation to the gradual loss of inhibition as the contents of the rumen pass on to the omasum or are absorbed

THE PASSAGE OF FOOD THROUGH THE ALIMENTARY TRACT

The rate at which food passes through the alimentary tract is slow in ruminants when compared to other animals or man The technique introduced by Lenkeit and Habeck (1930) in which hay or straw stained in a suitable way is given and the stained particles appearing in the faeces are estimated at daily intervals has been used extensively A summary of the early work using this method is given by Lenkeit (1933) which indicates that the maximum excretion of stained food in the faeces occurs at about 24 hours in the horse and pig but at 48 hours in the sheep Passage of stained marker seems to be a little less rapid in the cow than in the sheep for Usuelli (1933) found that the maximum excretion occurred at three days and the accumulative excretion curves given by Balch (1950) indicate that the quantity excreted at between 24 and 48 hours is about the same as that excreted from 48 to 72 hours after administration The delay is due to the time spent in the rumen for about 90 per cent of stained particles introduced directly into the abomasum are recovered in the faeces within 24 hours

Balch (1950) has shown that when stained ground hay is fed to a cow otherwise fed on long hay it passes from the reticulo-rumen more rapidly than the long hay and is excreted more rapidly in the faeces (Fig 1) This is an indication that the passage of liquid in which small particles are suspended through the sac is more rapid than that of the

solid food and fine particles can be washed through the organ more rapidly than long particles. Castle (1956) has shown the same effect in young goats.

It is possible in anaesthetized sheep with rumen cannulae to wash the rumen apparently clean by repeatedly introducing and removing water through the cannula, yet when the organ is opened it may still contain a mass of clean hay if it has been fairly recently fed. If, on the other hand, the animal is fasted for 24 hours before this operation, the food in the rumen is sufficiently finely divided to leave in suspension with the water, and the organ can be really emptied and washed clean. The opening to the omasum is somewhat smaller than the diameter of rumen cannulae and so this experience is a convincing demonstration of the fact that the food in the rumen cannot move onwards from the organ until it has been disintegrated into small particles. The speed with which it disintegrates therefore will affect the time spent by food residues in the rumen. A sheep on a dry ration may drink from 2 to 3 litres of water a day (Evans, 1957)—some sheep drink considerably more—and the saliva may add from 5 to 14 litres of fluid. The flow of water into the reticulum and rumen, therefore, is considerable and Hydén (1961), who has calculated the fluid volume of the rumen contents of sheep and the rate at which fluid leaves the rumen from the decrease in concentrations of polyethylene glycol introduced into the rumen, estimates the average flow of fluid from the rumen to be of the order of 7 litres in 24 hours. He estimates also that from 37 to 66 per cent of the water entering the omasum was absorbed. This is a wide estimate and Briggs (1961), using a modified form of the method of Oyaert and Bouckaert (1961), found that about 5 litres of water flowed from the omasum to the abomasum per 24 hours in sheep fed on mixed meals and hay, which suggests the lower estimate is reasonable. Differences in food and other experimental procedures may account for the discrepancies. Hydén's estimate is consistent with that given by Gray, Pilgrim and Weller (1954) who calculated the quantity of water absorbed in the omasum from the starch/lignin and nitrogen/lignin ratios of the contents of the various parts of the stomach of slaughtered sheep. Bailey (1961) has assessed the total salivary secretions of cattle fed on different rations to vary from 98 to 190 l. per 24 hours; this quantity together with the drinking water and the water contained in the food gave a range of from 125 to 255 l. of water entering the rumen per 24 hours. Hydén (1961) calculated that 150–170 l. left the rumen of cattle per 24 hours and both these

during resting The behaviour of the parotid gland under these conditions and the total flow of saliva in cattle that were neither eating nor ruminating are described by Bailey and Balch (1961*a* *b*) The interesting feature of the resting rate of secretion of the mixed saliva as it appeared at the cardia was that although eating stimulated the flow the hour immediately after feeding was the period of lowest secretion thereafter the resting rate of secretion increased until the next meal The electrolyte composition of the resulting mixed saliva in cattle was very similar to that of the parotid glands which is to be expected for under these circumstances the secretions of the sublabial and submaxillary glands are negligible and these secretions are the only ones that differ markedly from those of the parotid as regards electrolyte content

The decreased salivary secretion following feeding may be due to the inhibitory effect of distension of the rumen with food and the subsequent increase in salivation to the gradual loss of inhibition as the contents of the rumen pass on to the omasum or are absorbed.

THE PASSAGE OF FOOD THROUGH THE ALIMENTARY TRACT

The rate at which food passes through the alimentary tract is slow in ruminants when compared to other animals or man The technique introduced by Lenkeit and Habeck (1930) in which hay or straw stained in a suitable way is given and the stained particles appearing in the faeces are estimated at daily intervals has been used extensively A summary of the early work using this method is given by Lenkeit (1933) which indicates that the maximum excretion of stained food in the faeces occurs at about 24 hours in the horse and pig but at 48 hours in the sheep Passage of stained marker seems to be a little less rapid in the cow than in the sheep for Usuelli (1933) found that the maximum excretion occurred at three days and the accumulative excretion curves given by Balch (1950) indicate that the quantity excreted at between 24 and 48 hours is about the same as that excreted from 48 to 72 hours after administration The delay is due to the time spent in the rumen for about 90 per cent of stained particles introduced directly into the abomasum are recovered in the faeces within 24 hours

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estimates give an indication of the extent of the flow of water to be expected

The movement of food through the rumen of cattle has been studied in detail and has recently been summarized (Balch, 1961)

The omasum is the most difficult part of the stomach to examine After death the solid material between the laminae has a dry matter varying about 20 per cent When barium sulphate is introduced into the rumen it can be detected in the omasum within half an hour As far as is known semi-liquid contents enter the omasum at regular intervals that appear to be related to the contractions of the reticulum and the material leaving the omasum is a fluid containing from 5 to 8 per cent dry matter according to Oyaert's (1955) and Brigg's (1961) observations Trickles of opaque material can be seen leaving the organ at irregular intervals and occasionally denser material may be seen in the region of the abomasum below the lower pole of the omasum Regular changes of pressure within the organ have been recorded and even though water absorption occurs within it (Gray *et al*, 1954) there is reason to suppose that there is a differential rate of passage for liquid and solid material through the organ and that the solid material between the laminae, consisting of finely divided particles, are assisted in their passage by the flow of liquid The omasum remains an enigma in some respects and its mechanical activity can only be surmised from the various scattered pieces of information available Recently, Stevens, Sellers and Spurrell (1960) have suggested that it serves as a two-stage pump, aspirating reticular contents into the omasal canal, pumping the more fluid contents from the canal into the interlaminal spaces, and finally expressing the contents from these spaces into the abomasum

The flow of food from the abomasum onwards is continuous although variation occurs in the total weight of contents in the abomasum, small intestines, caecum and colon of sheep fed a standard ration and slaughtered at two-hourly intervals throughout a 12-hour feeding cycle (Boyne, Campbell, Davidson and Cuthbertson, 1956) The abomasal contents double between 2 and 4 hours after feeding and thereafter decrease, the greatest quantity of digesta in the small and large intestines occurs 10 hours after feeding

Measurements of the rate of flow from the abomasum to the duodenum of sheep have been made by sectioning and closing the cut end of the first part of the duodenum and directing the flow through cannulae placed in the cut ends The cannulae are joined outside the

body wall by tubing and the flow may be measured in this way in sheep consuming food in normal quantities by opening the tubing and collecting the material that flows from the abomasum, measuring it and reintroducing it again into the second part of the duodenum (Phillipson, 1952*a*). This method has been used in Scottish Blackface sheep fed on 300 gm. hay and 200 gm. of a mixture consisting of 2 parts linseed meal and 1 part oats every 12 hours and the mean flow per hour measured from 4 sheep was 360 ml. (Hogan and Phillipson, 1960). A second experiment made on four more Scottish Blackface sheep fed on 750 gm. of hay—half being given at 7.15 a.m. and half at 4.15 p.m.—gave a mean volume of 398 ml. per hour (Harris and Phillipson, 1961). A method of measuring flow in a duodenal by-pass, made in the same way, with an electromagnetic flow meter, which allows the flow to be measured without opening the connecting tube, is described by Singleton (1961) who found a mean value of 475 ml. per hour for three Clun Forest sheep fed on hay. Singleton observed that about 10 per cent of the material flowing from the abomasum to the duodenum flowed back again through the 'by-pass' and his values are corrected for this 'retrograde' flow. Clun Forest sheep are larger animals than Scottish Blackface sheep and presumably eat more which may account for the higher values found. In the experiment of Harris and Phillipson (1961) the sheep received paper, impregnated with chromium sesquioxide, twice daily and estimates of the chromium appearing in abomasal contents passing to the duodenum per 24 hours indicated that the flow was not less than 90 per cent of that expected from the quantities of chromium sesquioxide given daily.

The pattern of flow was influenced by feeding and by rumination. The flow to the duodenum was depressed about 1 or 2 hours after the sheep received food but increased after sustained periods of rumination and periods of maximum flow occurred in the early morning and during the early morning feed. The pooled results from all sheep show a clear relationship between the time devoted to rumination and the quantity of abomasal contents passing to the duodenum.

experimental conditions Hyden, using polyethylene glycol to estimate the flow through the stomach estimated that in sheep in which 7 l left the rumen per day, 9 5 l flowed from the abomasum As some of the 7 l would be absorbed in the omasum this estimate is well in agreement with the experiments quoted here and the flow from the abomasum represents a mean value of just under 400 ml per hour

The only information on the quantity of material flowing through the terminal part of the ileum is that obtained by Hogan (1957*a*) who found, in sheep fed on hay with linseed and oats, that it was about half the quantity entering the duodenum

THE MOVEMENTS OF THE RETICULUM AND RUMEN

The descriptions given by Wester (1926) and Schalk and Amadon (1928) provide a general picture of the major movements of these organs in cattle These descriptions were based upon records of the pressure changes within the cavities of these organs, using cattle with permanent fistulae, combined with observations in the movements of the various parts that could be felt with the hand from inside the rumen More recent descriptions are given by Cornwall and Reid (1959) and Stevens and Sellers (1960) The most important features of the movements that can be felt are described below and represent a summation of published accounts together with the author's own experience The pressure changes that can be recorded by sensitive transducers from the reticulum and the anterior, dorsal and ventral sacs of the rumen have been illustrated by Cornwall and Reid(1959) The incidence of such pressure changes, however, vary with the activity of the animal (Phillipson and Reid, 1960) Four main sequences of pressure waves can be distinguished in the rumen between a biphasic contraction of the reticulum, namely (1) a wave of increased pressure confined to the dorsal sac (D) which always forms the first pressure wave of all subsequent sequences and starts during the second phase of the contraction of the reticulum, (2) the D wave followed by a wave of increased pressore in the ventral sac as soon as the D wave subsides (DV), (3) the D wave is followed not by an increased pressure in the ventral sac but by a further wave of increased pressure in the dorsal sac which is synchrooous with a brief 'spike' of pressure in the reticulum, anterior and ventral sacs (DSV), and (4) the pattern is the same as that described for (3) except that a wave of pressure in the ventral sac follows the primary D wave (DVSV)

Of these patterns (4) was most frequent during feeding, (3) during rumination and (2) during resting.

Both Wester (1926) and Schalk and Amadon (1928) described secondary patterns of movement in the rumen that were not preceded by a biphasic contraction of the rumen, and noted that an alternated activity of the rumen often occurred, namely the biphasic contraction of the reticulum is followed by the primary wave of contraction in the rumen, followed by a period of rest; the next biphasic contraction of the reticulum, however, was followed by a primary and a secondary contraction of the rumen. This description tallies well with that given by Phillipson and Reid (1960) although the primary wave in their classification may be represented by D of DV whilst the secondary wave is SV. When the incidence of primary (DV) or modified primary waves (D) are compared to the incidence of secondary waves (SV) it is seen that variation with the activity of the animal is mostly confined to the two types of primary wave of increased pressure and, in particular, to the modified primary wave (D) which is more frequent during rumination than during feeding and resting.

Palpation of the walls of the pillars of the rumen allow pressure waves to be related to movements of these structures. The D wave is the result of contraction of the anterior pillar in a high position, the longitudinal pillars and the posterior and dorsal coronary pillars of the rumen. The wall of the dorsal sac also appears to become more tense. The V wave represents the contraction of the anterior pillar in a low position, the longitudinal pillars and the posterior and ventral coronary pillars of the rumen; the whole wall of the sac also becomes more tense and presumably is contracting. The (S) wave corresponds to the D wave in many respects but the position of the anterior pillar is rather lower and the greatest force seems to be the contraction of the dorsal coronary pillars which is often accompanied by contraction of the dorsal blind sac. The final (V) wave corresponds to the first one. It is probable that some of the more liquid contents of the ventral sac move forward over the anterior pillar during V contractions as suggested by Cornwall and Reid (1959).

The behaviour of the blind sacs themselves cannot be detected by pressure changes within the main cavities of the dorsal and ventral sacs. Contraction of the dorsal blind sac follows contraction of the dorsal coronary pillars and if a secondary cycle of rumen contraction occurs the contraction of the sac again passes to a very strong contraction of the pillars. During feeding it is common for a second contraction of

the sac to follow the second contraction of the pillars The contraction of the dorsal blind sac itself is coincident with contraction of the main body of the ventral sac

The contractions of the ventral blind sac are more variable than those of the dorsal blind sac A contraction of the sac itself usually follows the first contraction of its coronary pillars during feeding, during the DSV pattern of pressure waves that occurs with rumination the sac contracts without being preceded by an appreciable contraction of the ventral coronary pillars and coincides with the secondary dorsal sac contraction. As the secondary dorsal sac contraction involves a powerful contraction of the dorsal coronary pillars which represents the final stage of the dorsal blind sac contraction, the contractions of both dorsal and ventral blind sacs overlap each other The ventral blind sae contraction that is common during rumination is followed by an exceptionally strong contraction of the ventral coronary pillars

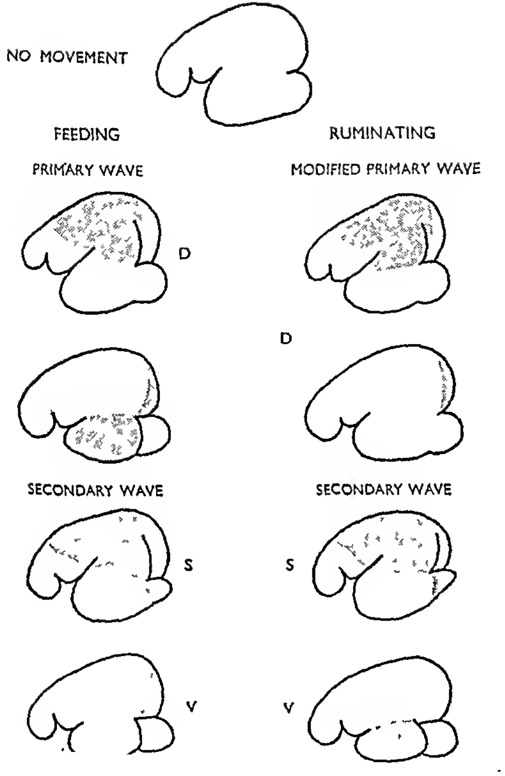
Table 7 1 gives the incidence of the patterns of pressure waves as

TABLE 7 1 *Incidence of pressure waves in the rumen (per cent)*

	(a)*					(b)†		
						Primary	Modified primary	Secondary
	D	DV	DSV	DVSV	Others	(DV)	(D)	(SV)
Feeding	1	27	5	56	11	55	4	41
Resting	10	35	25	22	8	41	25	34
Ruminating	22	28	37	6	7	25	43	32

* Total number of patterns analysed under (a) 5 995
† The analysis under (b) excludes the group 'Others of (a)

determined in four cows fed on freshly cut red clover Figure 7 1 represents diagrammatically the main movements of the rumen of cows and their sequence during feeding and rumination It should not be overlooked that variations that cannot be classified occur in the cow This is especially true of the blind sacs and of the two blind sacs the ventral is more variable than the dorsal When recording these movements it is a common experience that initially in any experiment great variation may be found presumably due to manipulations necessary when starting Variation is greater when the cow is restless than when she is placid. Change of activity from feeding to resting resting to ruminating or ruminating to resting may cause unusual variation during rumination and the early stages of feeding


NO MOVEMENT
FEEDING
RUMINATING
PRIMARY WAVE
MODIFIED PRIMARY WAVE
D
D
SECONDARY WAVE
SECONDARY WAVE
S
S
V
V

the activity is most stable, providing the animal is not distracted The descriptions given here apply to the periods of stability in pattern that can be recognized during rumination and feeding rather than to periods of transition, distraction, or of resting It would be unwise to assume that the small ruminants would give the same patterns of activity as those found in cattle The same types of movement seem to occur but their frequencies may be dissimilar

RUMINATION

Cattle and sheep spend approximately one-third of their time ruminating The distribution of ruminating periods throughout the daylight hours varies but the greater part of rumination in sheep occurs during the period 12 noon to 12 midnight (Gordon, 1958) The material regurgitated seems to come more from the anterior sac of the rumen than from the reticulum and the material entering the oesophagus has the consistency of a coarse gruel Coarse food recently ingested does not form the bolus as it passes backwards to the rumen. After rechewing, the solid material is swallowed again to the reticulo-rumen sac Liquid is swallowed at intervals during chewing and also returns to this sac

The mechanism of regurgitation has been the subject of considerable dispute which reached a climax at the end of the nineteenth century Two principal concepts were put forward. Colin (1886) contended that increased pressure in the reticulo-rumen sac was the principal force moving semi-fluid food into the oesophagus, Toussaint (1875) contended that a fall of pressure in the thorax due to an inspiratory effort with a closed glottis is translated to the lumen of the thoracic oesophagus so that a fall of pressure in this organ causes food to flow into it. Most of the subsequent work supports the second view and it is easy for anyone to insert his hand into the rumen of a fistulated cow, to work the hand forward to the region of the cardia, to stimulate rumination by stroking the wall of the reticulum with the fingers and then to feel the movement of food through the cardia When this is done the impression gained is that food is drawn into the oesophagus rather than pushed in by a rise in pressure in the region of the cardia. A preliminary contraction of the reticulum occurs before the usual biphasic contraction and is accompanied by the entrance of food into the oesophagus, immediately after this the usual biphasic coutraction of the reticulum follows During regurgitation the cardia dilates and a funnel shape is formed through which food passes rapidly There

is no doubt about the fall in pressure in the thorax; ample evidence supports this concept, while a fall in pressure also occurs in the thoracic oesophagus (Stigler, 1931). Bell (1958) has recently recorded a sharp rise in pressure in the 'antrum' of the rumen during regurgitation in intact goats and considers that this materially assists the passage of food into the oesophagus. Stevens and Sellers (1960), however, have re-investigated the pressure gradients in ruminating cattle with rumen fistulae and find little evidence that increased pressure in the region of the cardia occurs; they conclude that the movement of food into the oesophagus is due mostly to the decreased pressure within its lumen. Whether the oesophagus itself actively contracts and owing to its attachment to the diaphragm forms the funnel shape as suggested by Wester (1926) is not proven. The oesophagus consists of striated muscle and it can be seen to dilate in its thoracic portion during regurgitation (Czepa and Stigler, 1926). The more recent observation of Webster and Cresswell (1957) in which trained sheep fitted with a tracheal cannula were examined showed that they could ruminate just as easily with an open trachea as a closed one: an observation that suggests that a combined contraction of the oesophagus and diaphragm is possibly the most important operative force concerned.

Although regurgitation normally occurs immediately after the first of the three contractions of the reticulum it may occur at other times (Downie, 1954). By inserting the hand into the rumen and placing it in such a position that it obstructs the flow of food into the oesophagus the author has found it possible to induce a cow to regurgitate as many as four times in between each biphasic reticulum contraction. The efforts appeared to be made voluntarily to obtain enough cud to chew and did not appear to be related to any particular stage of contraction or rest in the reticulum or rumen. It is also possible for regurgitation to occur in animals in which the reticulum movements have been suppressed by injection of atropine (Wester, 1926; Duncan, 1954) so that contraction of the reticulum cannot be considered as an essential part of the mechanism. Contraction of the diaphragm or abdominal muscles, however, may aid regurgitation by increasing intra-abdominal pressure.

(Washburn and Brody, 1937) and the evidence indicates that it is formed by reduction of carbon dioxide Succinate, formate and hydrogen are hydrogen donators for this reaction when it is accomplished by rumen bacteria (Beijer, 1952) The rate of conversion of hydrogen and carbon dioxide to methane by rumen organisms is more rapid than the formation of carbon dioxide from formate, a reaction that is quantitative, and this provides a reasonable explanation for the virtual absence of hydrogen in the rumen gases and of formate in the fatty acid mixture of normal animals (Carroll and Hungate, 1955) Hydrogen appears in the rumen gases in quantity after a period of fast (Pilgrim, 1948) and under these conditions methane is absent The change from hydrogen to methane occurs over a few days when feeding is resumed

The remainder of the rumen gas is composed largely of carbon dioxide derived from fermentation of carbohydrates, and released as a result of neutralization of organic acids by salivary bicarbonate Traces of nitrogen and oxygen may appear in the rumen as the time after feeding increases (Washburn and Brody, 1937) This is due presumably to swallowed air but oxygen is rapidly removed for the proportion of nitrogen to oxygen is much greater than in atmospheric air

The early observations on belching, summarized by Mangold (1929), show that it is more frequent after feeding and during rumination than when the cow is at rest The frequency of belching has an unmistakable relationship to the frequency of rumen movements that can be observed in the left lumbar triangle An association between belching and the secondary wave of contraction of the rumen was established by Wester (1926) and has ample confirmation (Weiss, 1953, Williams, 1955, Reid, 1957) Changes in the frequency of secondary rumen contractions were observed by Williams (1955) on commercial dairy cows, and on observations made on over 250 animals showed that the secondary contraction occurred in 74 per cent of the animals examined

The association of the secondary rumen contraction with belching suggests that the stimulus that causes the one may cause the other Weiss (1953) postulated that pressure in the posterior part of the rumen caused belching but recent work (Ash and Kay, 1959, Comline and Titchen, 1957) on the sensitivity of the reticulo-rumen sac indicates that although tactile stimulation of the posterior pillar may reflexly cause an increase in the incidence of reticulum contractions and salivation, the anterior pillar and particularly the reticulo-ruminal fold, and the wall of the reticulum itself, are more sensitive The propulsion of

gas from the dorsal sac to the region of the cardia occurs during the secondary rumen contraction and Stevens and Sellers (1960) observed that the cardia opened during this contraction. The actual stimulus that causes the cardia to open so that gas passes into the oesophagus is not understood, for belching sometimes occurs immediately after the biphasic contraction of the reticulum.

Dougherty and Meredith (1955) observed belching by cinefluorography when opaque fluid was in the stomach of a sheep and gas was introduced into the rumen in a steady stream. They observed that the obstruction could occur: (1) at the cardia; (2) in the thoracic oesophagus about two inches anterior to the cardia; and (3) at the upper end of the oesophagus immediately posterior to the pharynx. Dougherty and Habel (1955) give the series of events as follows: (1) a biphasic contraction of the reticulum occurs; (2) contraction and raising of the reticulo-ruminal fold; (3) the passage of gas forward from the rumen which may completely fill the reticulum; (4) increased contraction and dilatation of the oesophagus; (5) relaxation of the cardia and of the area immediately anterior to it; (6) continued closure of the upper end of the oesophagus so that the oesophagus fills with gas; (7) closure of the cardia and its adjacent area of oesophagus; and (8) closure of the glottis causing a transient rise in intrapleural pressure which aids the oesophageal musculature to clear the oesophagus rapidly through the relaxed upper end of the oesophagus. It is of considerable interest that Dougherty and Habel (1955) observed that if the rumen was filled with water so the cardia remained submerged and belching was then stimulated with gas insufflation, the oesophagus filled with liquid but the cranial end of the oesophagus did not relax, suggesting that the response to liquid and gas was different in an important way. In bloating, belching persists in the early stages as pointed out by Johns but it is possible that as the rumen becomes distended with foam, foam rather than gas enters the oesophagus and under these circumstances may be unable to escape if foam has the same effect on the upper end of the oesophagus as that found for liquid.

With sheep with a normally filled rumen the events described when gas is not introduced into the rumen are not so obvious; however, the fall in the fluid level of the reticulum occurs regularly; the reticulo-rumenal fold forms a partial and temporary barrier immediately after the reticulum contraction in the manner described by Dougherty and Meredith (1955) and the activity of the cardia and the sensitive area of the oesophagus immediately caudal to it can be observed (Benzie and

Phillipson, 1957) In addition dilation of the reticulum, as suggested by Weiss (1953), can sometimes be observed

THE CHEMICAL CHANGES IN THE RUMEN

The bacteria and protozoa in the reticulo-rumen sac live on the food eaten by the animal and two classes of materials are formed in the rumen as a result of their metabolism These are (1) the complex molecules that go to make up bacterial and protozoan cells, and (2) the simple by-products of their metabolism The extent to which food is digested in this way has been estimated in cattle by Balch *et al* (1955) and in sheep by Hogan (1957*b*) who concluded that about 70 per cent of the digestible dry matter disappeared in the rumen with cattle or in the whole stomach with sheep The by-products of microbial metabolism in the rumen include the lower steam volatile fatty acids ammonia B vitamins, carbon dioxide and methane Estimates of the total quantity of volatile acids in the rumen of sheep fed on grass (Elsden Hitchcock Marshall and Phillipson 1946) or on a dry ration (Boyne *et al* 1956) vary from 0 8 to 1 1 equivalents The total weight of individual acids in the reticulo-rumen sac of two cows fed on 16 lb hay and 20 lb of a concentrates mixture consisting of flaked maize 10 parts weatings 7 parts decorticated groundnut cake 3 parts with 0 5 per cent mineral mixture were determined by Balch *et al* (1955) and the mean figures are acetic acid 314 mg propionic acid 160 gm and butyric acid 101 gm Other C_4 acids together with C_5 and higher acids amounted to 59 gm when expressed as valeric acid These quantities give no indication of the total turnover but even so they are large enough to indicate that these acids are an important product of fermentation in the rumen

THE PROTOZOA

The first thing that is obvious when a drop of warm freshly-drawn rumen liquor is placed on a slide under the microscope is the ciliated protozoa which swim rapidly among the plant debris Their activity persists for some time provided the preparation is kept warm There are five principal genera to which these organisms are assigned and classifications are given by Becker and Talbott (1927) and Mangold (1929) Estimates of the numbers present indicate that these are influenced by the composition of the food and Mowry and Becker (1930) record counts of about 200 000 per ml for sheep fed on hay alone and 2 000 000

per ml. for sheep fed on hay with a supplement containing protein and starch. Similar variations in relation to diet were observed by van der Wath and Myburgh (1941) in South Africa. The frequency of feeding even though the same quantity of food is eaten per day also seems to influence the concentrations of protozoa in the rumen (Moir and Somers, 1956). The contributions made by the rumen ciliate population to the total chemical changes occurring in the rumen have not been assessed but sufficient is known of their metabolism to indicate that these contributions are likely to be appreciable. Certain species belonging to the order Holotrichida are known to ferment soluble fodder carbohydrates rapidly forming, besides volatile acids, a polysaccharide within them in the form of granules identified as an amylopectin (Forsyth, Hirst and Oxford, 1953). This substance can form up to 70 per cent of the dry weight of these organisms. This activity is unaffected by the presence of high concentrations of streptomycin so that there is no doubt that the enzymes concerned are produced by the ciliates themselves (Heald and Oxford, 1953). The storage amylopectin is metabolized in the absence of soluble carbohydrate to give rise to a mixture of acetic, butyric and lactic acids, carbon dioxide and hydrogen (Heald and Oxford, 1953). Many of the ciliates ingest starch granules if these are small enough to enter their pharynx, and starch granules are also converted to amylopectin (Sugden, 1953). Ciliates also seem to be responsible for some of the ammonia present in the rumen (Warner, 1956).

Gruby and Delafond (1843), who discovered the ciliates, also noted that these organisms were dead and disintegrating in the abomasal contents; an observation that has been repeatedly confirmed. Dead ciliates have also been found in omasal contents (Ferber, 1928; Masson, 1950). The substance of these organisms, therefore, is available for digestion in the abomasum and small intestines and so contributes to the nutrition of their host.

provides larger figures still but with less variability There is no certainty that all viable bacteria will grow in any one medium and in direct microscopical counts there is no certainty that all the cells counted are viable so that both methods have their limitations The pitfalls of trying to make counts are emphasized by the work of Bryant and Burkey (1953) who give comparisons of the effect of variation in technique in handling and diluting the samples upon the counts obtained They give 1,700 million per ml as a representative figure for the concentration of bacteria estimated by dilution counts using a media containing rumen contents under an atmosphere of carbon dioxide and 20,200 million per ml for the concentration estimated by direct microscopic counts of diluted stained smears of a known aliquot Oxford (1956) considers that a count of 100 million bacteria per gm of rumen contents is an indication that a given class of bacteria is present in abundance and that counts of one million per gm indicates that the class may be of some importance but is not plentiful Wilson and Briggs (1955) have estimated the number of viable bacteria per gm of rumen contents obtained from fistulated cows fed on various rations and find the majority of values are from 100 to 10,000 million bacteria per gm They noted that counts for samples taken from different parts of the rumen showed wide variation

Gall, Stark and Loosli (1947) found from 50,000 to 100,000 million bacteria per gm of fresh rumen contents of sheep using a direct counting method This method has been used extensively by Moir and his colleagues in Western Australia in order to examine some of the probable factors that may influence the population in the rumen They worked on samples of rumen contents withdrawn by stomach tube and estimated the so-called free bacteria, i e the bacteria present in the liquor and not attached to plant fragments Representative figures for sheep are from 20 to 40 million per mm ^{3} (Williams and Moir, 1951)

The variability of the concentration of bacteria when this is made by cultural dilution methods has led to the opinion that even though there may be a dietetic effect this is largely overshadowed by variation due to unrecognized causes Far less variability has been found by the direct counting techniques and here there is indication that variation in the concentration related to the food does occur Moir and Williams (1950) observed that increasing the protein of the ration from 15 to 133 gm per day in rations containing starch caused a closely related increase in the 'free bacterial count' The inclusion of starch,

however, seems to be essential if this is to occur as increasing the protein of rations with no starch supplement is ineffective in this respect (Williams, Nottle, Moir and Underwood, 1953). The addition of starch to low protein rations depresses the bacterial count. Moir (1951) also noted a seasonal fluctuation in the direct count in stomach tube samples taken from grazing Merino sheep throughout the year in Western Australia. Seasons of rapid growth of grass—the warm wet seasons—were associated with an increased total count.

There is reasonable evidence to indicate that change in the proportion of one kind of organism to another does occur in the rumen. Bryant and Burkey (1953) found that the proportion of cellulose-hydrolysing organisms fell to about 5 per cent of the total numbers isolated when a concentrates ration was fed to cows but increased to 28 per cent when wheatstraw alone was fed; it remained at about 8 per cent of the total for other rations. The changes in the types of bacteria in the rumen of sheep when excessive quantities of starch or glucose are given have been described by Hungate, Dougherty, Bryant and Cello (1952) and for sheep fed a ration rich in flake maize by Masson (1950). Under both circumstances a fermentation, characterized by the production of lactic acid in large quantities, is set up. *Streptococcus bovis* was demonstrated to be present in large numbers by Hungate *et al.* (1952) and in flake-maize fed sheep a sporulating rod—presumed to be *Clostridium butyricum*—was found.

Baker studied the associations between bacteria and plant fragments extensively by microscopic examination and this technique has been applied to the contents of the large gut of the guinea-pig, the rabbit, the pig and the horse as well as to the rumen contents. Plant fragments are attacked by cocci which erode areas from the plant tissues. The use of polarized light indicated that disintegration of cellulose occurs in the areas immediately adjacent to the bacteria. The bacteria concerned invariably possessed the property of staining blue with iodine indicative of polysaccharide formation. This property is not confined to organisms adherent to plant particles in the rumen but is common to a great many of the bacteria in the organ. Organisms that can be recognized on morphological grounds have been described by Baker (1942) and a classification is offered by Moir and Masson (1952). The most detailed morphological account of the rumen organisms as they appear when photographed in the living state in ultraviolet light is given by Smiles and Dobson (1955) and the structural detail revealed was helpful in studying the disintegration of certain

organisms in the abomasum A large number of bacteria in the rumen are facultative anaerobes and Heald and Oxford (1953) estimated the concentration of such organisms as 100 million per gm of rumen contents in hay-fed sheep Nearly half of the strains isolated proved to be streptococci of which 82 per cent resembled *Str bovis*, 6 per cent *Str faecalis* and 12 per cent were unidentifiable Staphylococci were also isolated and also coliform organisms of the intestinal types A large Gram-negative sarcina-like organism named *Sarcina bakeri* was isolated and a few strains of Gram-negative rods (Mann Masson and Oxford, 1954) Many of the streptococci resembling *Str bovis* and other streptococci have capsular polysaccharides that are serologically active (Hobson and MacPherson, 1953), and the Neufeld capsular swelling reaction has been used to distinguish between isolated strains and to demonstrate the presence *in situ* in the rumen contents (MacPherson 1953) Labelling the specific antibody with fluorescein isocyanate enables bacteria on which the antisera is absorbed to be seen in ultra-violet light (Hobson Mackay and Mann, 1955)

THE DIGESTION OF CELLULOSE

The isolation and study of cellulose-fermenting bacteria from the rumen by Hungate (1944 1946 1947) and Sijpesteijn (1951) gave an indication of the kinds of organism concerned and information of their requirements and metabolism Also the more recent work of Bryant and Burkey (1953) indicates the proportion of the total population of the rumen of cattle that possess cellulolytic properties They isolated 62 strains of cocci some of which produced capsular material and some a yellow pigment, and 56 strains of slender rods occurring in pairs but not in chains, some of the rods formed 'rosette' clusters giving a similar appearance to the 'rosette' bacteria described by Baker (1942) The 118 strains represent about 13 per cent of the total strains of bacteria —896 in all—that were isolated The variation of the numbers of cellulolytic bacteria in relation to diet has been mentioned earlier

The initial stages of the degradation of cellulose by bacterial enzymes is unknown although there is little doubt that the end products of fermentation by mixed rumen organisms is a mixture of acetic and propionic acids together with carbon dioxide and methane Certain strains (Hungate 1947) produce hydrogen not methane, but in the rumen free hydrogen is taken up in other reactions and may serve as a source of hydrogen for methane formation Approximately equal amounts of acetic and propionic acids are formed by the fermentation

of filter paper by mixed rumen organisms (Elsden, 1945; Marston, 1948; Louw, Williams and Maynard, 1949). Marston calculates that about 6 per cent of the energy of cellulose disintegrated is incorporated in the bacteria themselves.

The presence of C_5 and C_6 acids is reported by Bentley *et al.* (1954) as stimulating cellulose fermentation and Bryant and Doetsch (1954) find that one straight chain acid and one branched chain acid give the best growth with *Bacteroides succinogenes.* The possibility of other factors is discussed by these workers.

THE FERMENTATION OF STARCH

Bryant and Burkey (1953) in their study of the rumen organisms of cattle fed on six different rations found that of the strains isolated from the rumen from 32 to 56 per cent hydrolysed starch on all rations except when cows were fed straw only. Then the proportion dropped to less than 20 per cent. Among the organisms isolated was *Streptococcus bovis.* Higginbotham and Wheater (1954) have found *Str. bovis* to be constantly present in the rumen of cattle on stall-fed rations or at pasture but in comparatively low concentrations, *i.e.* 0·1–10 millions per ml. Perry, Wilson, Newland and Briggs (1955), however, found streptococci in the rumen of stall-fed cattle in the concentration of 100 million/ml. when hydrolysis of starch was the one criteria used in identification. Even higher counts, 1,000–100,000 million ml. were found in grazing animals. There appeared to be a reciprocal variation between streptococci (all of which were identified as *Str. bovis*) and lactobacilli (presumptive). The former were numerous at grass but not when stall-fed rations were given when lactobacilli became dominant.

Digestion of starch in the rumen is extensive and the quantity of food starch leaving the rumen, except possibly when rations contain excessive quantities, is not large. Gray *et al.* (1954) found very little starch in the abomasal contents of sheep fed on wheaten hay with or without potatoes. The starch content of the rations varied from 3 to 150 gm. daily (these authors are careful to point out that the expression 'starch' includes capsular polysaccharides of the kind described by Hobson and MacPherson (1953) and amylopectins when applied to stomach contents), whilst on the basis of 'starch'/lignin ratios it is calculated that the amount of starch passing through the abomasum daily is only 1–8 gm. This estimate agrees with that of Heald (1951) who determined the glucose-containing carbohydrate of the abomasal

contents of sheep and estimated the quantity passing from the abomasum per 24 hr to be in the region of 5 gm in sheep fed on hay

The products of bacterial degradation of food starch are short-chain fatty acids but the establishment of a lactic acid fermentation with starch feeding is known to occur (Hungate *et al*, 1952, Phillipson 1952*b*, and Balch and Rowlands, 1957) The occurrence of lactic acid in the rumen is also associated with a reduced concentration of acetic acid and an enhanced concentration of propionic acid in both sheep and cattle, conditions that are also associated with a depression of the butter-fat concentration in cow s milk

THE FERMENTATION OF SUGAR

Numerous streptococci lactobacilli and other bacteria are capable of fermenting fodder sugars In addition the holotrich and certain heterotrich protozoa perform the same function in the rumen The result is that the ruminant absorbs little or none of the soluble sugar of the ration but instead obtains the short-chain fatty acids that are formed, notably acetic and propionic acids Lactic acid may appear temporarily in the rumen where foods such as mangold-wurzels containing sugar are fed, or where large experimental doses of glucose or cane sugar are given Lactic acid however, is not stable in the rumens under these conditions and bacteria capable of fermenting it to acetic and propionic acid are usually present (Elsden 1945, Johns 1951)

Less is known of the pentose sugars Mixed rumen organisms are known to be able to ferment xylose, and pentosan isolated from wheat flour was shown to be rapidly fermented (Howard 1955) The products of xylose fermentation are acetic and propionic acids, rather less butyric (including *iso*butyric acid) and traces of formic acid

PROTEIN

Proteolysis by mixed rumen bacteria was found by Sym (1938) and Warner (1956), it is also known that protozoa-rich fractions of rumen contents possess proteolytic properties (Warner, 1956) Appleby (1955) found that the most frequently occurring organisms with proteolytic properties were facultative anaerobes of the genus Bacillus, nineteen out of twenty-four strains were identified as B *licheniformis* which were found in dilutions of $1/10^4$–$1/10$ Other proteolytic organisms isolated were Clostridia, Gram-negative rods, Corynebacteria and Micrococci The proteolytic activity of rumen content of sheep was found by Warner (1956) to be consistently high irrespec-

tive of whether the sheep was fed on a low-protein hay or on a high-protein ration. Blackburn and Hobson (1960*a*, *b*) noted that the proteolytic activities of various fractions of rumen contents were similar so that the activity presumably was evenly distributed throughout the rumen organisms present. They obtained similar results to those of Appleby (1955) by the use of isolation and identification methods and they conclude that the concentrations of organisms recognised by these techniques as possessing proteolytic properties, represent only a small fraction of the proteolytic organisms present. Even though the proteolytic power of rumen liquor does not seem to be markedly influenced by the protein content of the food, the deaminative activity may be increased when protein-rich foodstuffs are fed (el Shazly, 1925*a*, *b*; Warner, 1956). The free amino acid concentration in rumen liquor is generally small (Lewis, 1955; Chalmers and Synge, 1954) although transient increases occur after heavy protein feeds. Synge (1957) as a result of the studies on the degradation of protein in the rumen and of the value of various protein sources in milk production emphasizes 'the usefulness of measuring the time course of evolution of ammonia in the rumen as a first exploratory step in studying protein utilization in the ruminant' (Fig. 7.2).

Recent studies on the nitrogen requirements of a large number of rumen bacteria show that 'in vitro' only a minority have an absolute requirement for amino nitrogen. The large majority can utilize ammonia nitrogen and the presence of ammonia nitrogen in the media is obligatory for growth for certain organisms. The incorporation of ammonia nitrogen in mixed rumen organisms was found by Warner (1956); in starch-fermenting bacteria from the rumen by Phillipson, Dobson and Blackburn (1959) and in several of the cellulolytic bacteria by Bryant (1960) and Bryant and Robinson (1961). It is also known that urea can substitute for a considerable part of the protein of the ration and a voluminous literature exists on this subject. The presence of a urease in rumen liquor (Pearson and Smith, 1943*a*, *b*) and the production of ammonia from urea suggests that deamination of urea is the first step in at least one route whereby its nitrogen is incorporated into bacterial protein. Sheep have been maintained on rations in which virtually the sole source of dietary nitrogen is in the form of urea and have made weight increases (Thomas, Loosli, Williams and Maynard, 1951) but perhaps the most telling evidence is that given by Land and Virtanen (1959) who administered ammonium salts in which the nitrogen contained 61 atom % of ^{15}N to lactating

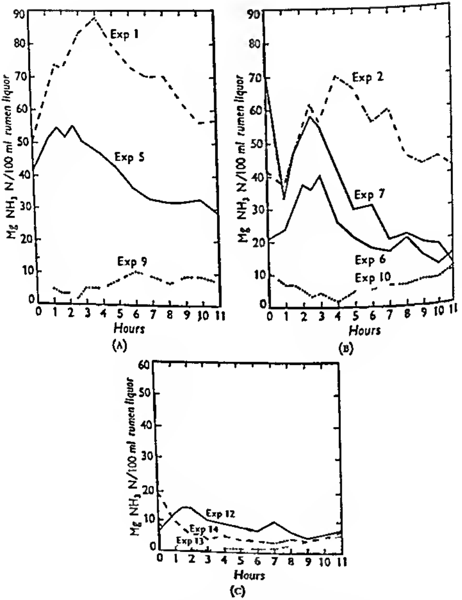


FIG 72

(A) Concentration of ammonia in rumen liquor of sheep no 716 receiving casein (Exp 5) groundnut meal (Exp 1) and flaked maize (Exp 9) as main source of protein.

(B) Concentration of ammonia in rumen liquor of sheep no 718 receiving casein (Exps 6 and 7), groundnut meal (Exp 2) and flaked maize (Exp 10) as main source of protein.

(C) Concentration of ammonia in rumen liquor of sheep receiving all hay diet (Exp 12), hay and ground maize diet (Exp 13) and hay and flaked-maize diet (Exp 14)

(From Annison *et al*, *J agric Sci*, 1954 44, 270)

cows and showed that excess ^{15}N was incorporated in the amino acids of the milk. They consider that possibly 40 per cent of the ammonia nitrogen given was utilised for protein synthesis as the quantity excreted in the urine and faeces was about 60 per cent of that administered. The contribution that bacteria themselves make as an end product of digestion in the rumen was discussed by Thaysen (1945) who gave as a very conservative estimate a figure of 400 gm. of dry bacterial substance passing to the omasum per 24 hours. This is certainly an underestimate as it ignores the protozoa. It does go quite a long way, however, to substantiate the opinion, frequently expressed by Baker, that the cell substances of the micro-organisms of the rumen are quantitatively important sources of nourishment to their host.

The range for the concentration of ammonia nitrogen in sheep grazing New Zealand pastures was found by Johns (1955) to be from 35 to 130 mg./100 ml. of rumen liquor. The sheep in question were placed in stalls overnight so that fasting levels could be obtained before the animals were turned out to pasture and samples were taken again about six hours after they were turned out to pasture. Williams and Christian (1956*a*, *b*) in an area further north in New Zealand report values in sheep which had free grazing from 9·1 to 46·6 mg. ammonia nitrogen/100 ml. liquor. These values are similar to those for high protein rations fed indoors.

THE COURSE OF DIGESTION IN THE RUMEN

The fluctuation of the concentrations of the various soluble constituents of rumen liquor has been studied in the the rumen of sheep and cattle usually by withdrawing samples of the liquor through permanent cannulae placed in the organ. The first feature is that the concentration of total volatile fatty acids varies inversely with the pH of the contents (Briggs, Hogan and Reid, 1957; Balch and Rowlands, 1957) (Fig. 7.3); the exception occurs when there is an accumulation of lactic acid which may be rapid and transient and which is associated with a sharp fall in pH which again varies inversely with the lactic acid concentration. Briggs and his colleagues found that the relation between pH and lactic acid was as significant as that between pH of volatile acids. The increases of total volatile acid concentration are small following feeds of hay but large after feeding concentrates. Sheep or cattle grazing pasture grass have a consistently lower pH of the rumen contents than when fed on dry indoor rations unless these are rich in starch (Phillipson, 1942, 1952*a*, *b*; Balch and Rowlands,

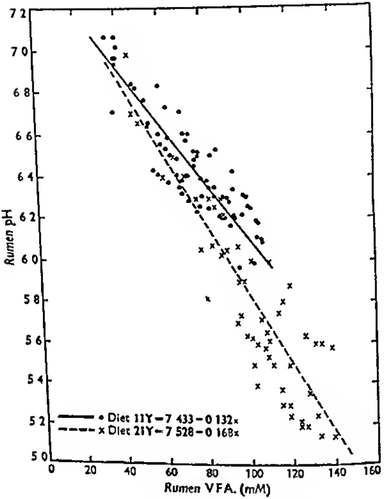


FIG 7 3

Diet 1 = 510 gm wheaten chaff plus 170 gm lucerne chaff
Diet 2 = 150 gm wheaten chaff 50 gm lucerne chaff 480 gm wheat and 0-85 gm. wheaten starch. (From Hogan and Reid *Aust J agric Res* 1957 8 p 674)

1957) when a lactic acid fermentation is set up and a low pH is found in the rumen.

The proportions of the various fatty acids present are not entirely constant relative to one another throughout a digestion cycle, and following feeding it is usual to find the proportion of propionic acid increasing at the expense of acetic acid (Gray *et al*, 1954, Balch and Rowlands 1957, Briggs *et al*, 1957) Sheep at grass have about 53–72 per cent acetic acid and 15–27 per cent propionic acid in the rumen

liquor; the remainder consisting of *n*- and *iso*butyric acids and C_5 (Johns, 1955). Only traces of lactic acid are present. Ammonia concentrations increase after feeding, especially if the food contains readily available protein or other nitrogenous compounds. As saliva contains appreciable quantities of urea (MacDonald, 1948) and as feeding stimulates salivary flow a part of the ammonia in the rumen—even though this may be only a small part—is probably of salivary origin. As the submaxillary and sublingual glands contain mucoprotein this may also be a source of ruminal ammonia but there is as yet no information on the fate of salivary proteins in the rumen or of their possible significance in contributing amino nitrogen for bacterial metabolism.

Gas production following feeding is large; carbon dioxide is derived from fermentation and from the neutralization of organic acids by salivary bicarbonate. Another possible source is from the plasma as an exchange mechanism concerned with organic acid absorption.

that the rumen epithelium is relatively impermeable to hydrogen and hydroxyl ions, moderately permeable to bicarbonate, and readily permeable to carbon dioxide (Ash and Dobson, 1961) When fatty acid is absorbed an increased consumption of carbon dioxide occurs, superimposed upon an increased rate of appearance of bicarbonate in the rumen contents, which suggests that half the fatty acid absorbed from solution with a pH of 7 is absorbed as free acid, and half as the anion Neutralization of fatty acids in the rumen, therefore, is due not only to the bicarbonate content of the saliva but also to the exchange mechanism studied by Ash and Dobson

The fatty acids and ammonia are always present in the rumen in concentrations higher than that of blood and as the epithelium is permeable to them absorption is continuously occurring There is some indication that acidity may depress the adsorption of ammonia (Hogan, 1957*a, b*) The composition of the acids in the rumen and in the venous blood leaving the rumen is similar except that the blood contains less butyric and more acetic acid A comparison made on grass-fed sheep is given in Table 7 2

TABLE 7.2 *Mean values for three grass-fed sheep*

	Rumen contents per cent	Venous blood from the posterior vein leaving the rumen per cent
Acetic	63 1	69 3
Propionic	17 6	18 1
Butyric	14 0	6 4
Higher acids	5 1	6 2

The values for venous blood in Table 7 2 were corrected for performed acetate circulating in the arterial blood Similar results have been obtained by Annison, Hill and Lewis (1957) who used the elegant technique of portal vein catheterization in conscious sheep to compare portal blood with carotid blood and rumen contents of normally feeding sheep These figures which are not corrected for preformed acetic show greater trends in the same direction as those given in Table 7 2 Portal blood also contains fatty acids from intestinal sources although the close relation observed between rumen and portal blood concentrations suggests that the quantity derived from the lower part of the ileum and large gut is small in comparison to that of the rumen

Schambye (1955*a, b*) estimated the blood flow in the portal vein of sheep to be from 31 to 44 ml /min /kg and combining this with estimates of excess volatile fatty acids and glucose in portal blood com-

pared to carotid blood, he calculated that the volatile acids absorbed per hour were 129–153 m.equiv. or 1·5–2·9 equiv. per 12 hours which was the interval between feeds. When these values are expressed as calories they account for well over half of the heat expressed by an adult sheep during a fast. Uptake of glucose from the alimentary tract is small in comparison to the uptake of volatile fatty acids (Schambye, 1955*a*, *b*; Annison *et al.*, 1957).

Of the inorganic constituents of the rumen the most interesting is sodium. Chloride and potassium in physiological concentrations behave as passive ions. Vegetable food and pasture grass contain a lot of potassium and comparatively little sodium and this difference is enhanced by potassic manures. High potassium concentrations in the rumen have the effect of increasing by some 8–10 mV the potential difference between the blood and the rumen contents (Dobson, 1959). The sodium eaten in the food is considerably augmented by sodium secreted in the saliva; even so, the concentration in the rumen has not been known to exceed that of the plasma (Parthasarathy, 1952). Estimates made by Dobson (1961) indicate that about 1·25 equiv. of sodium enter the rumen of sheep daily, and of this only a small fraction is in the food, the bulk being present in the saliva. About 0·5 equiv. leave the rumen per day, indicating an adsorption of about 0·7 equiv. per day from the reticulum and rumen. Irrespective of the sodium entering the intestine in the secretions, about 15–30 m.equiv. are excreted in the faeces which is an indication of the efficiency of sodium absorption in the gut. The work of absorption in relation to sodium is considerable as sodium has to pass to the plasma against both an electrical and chemical gradient. Dobson (1959) estimates the work done by the rumen epithelium in absorbing sodium is not less than 0·2 μW per mg. dry weight of the tissue.

In anaesthetized sheep in which the rumen is isolated and filled only with solutions of known tonicity, water moves into the rumen when hypertonic solutions are introduced and out of the rumen when hypotonic solutions are introduced. The point at which volume equilibrium is reached and little or no volume changes can be detected is when solutions of 0·175 m.mol./l. are introduced into the rumen (Dobson, 1961).

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of the liquid and solid matter takes place It is common knowledge that the dry matter content of the omasal digesta of slaughtered animals is greater than that of the reticular or abomasal contents Recently Badawy, Campbell Cuthbertson Fell and Mackie (1958) found that the dry-matter content of the material increased from the omasal sulcus to the greater curvature of the organ and from the reticular end to the abomasal end Volatile acids are absorbed from this organ and their concentration in the material present parallels the changes in dry matter so we may assume that opportunities of absorption of both water and volatile acid are greater along the greater curvature This probably means that it takes a longer time for food to traverse the greater curvature of the organ than the lesser curvature

Ekman and Sperber (1953) observed that in the omasum of cows the bicarbonate concentration decreased and the chloride concentration increased in the digesta as it was taken from the reticular end or the abomasal end This confirms the overall increase in chloride concentration observed in the omasum of sheep (Masson and Phillipson 1952) The solid material that enters the abomasum therefore, has lost some of its volatile fatty acid and bicarbonate and gained chloride in its place (Briggs 1961) The concentrations of ammonia leaving the omasum however, are very similar to those in the rumen.

One further change has been reported by Oyaert (1955) who estimated that considerable losses of sodium occurred in the organ Ions such as calcium magnesium and inorganic phosphorus are slightly concentrated (Garton 1951)

THE SECRETION OF GASTRIC JUICE FROM THE ABOMASUM

The contents of the abomasum of sheep fed on dry foodstuffs indoors under normal circumstances are always acidic and the pH of the contents usually varies around a value of 3 this is true also for the sheep at pasture although here exceptions have been recorded when the acidity was less (Garton 1951) The fact that the flow of predigested food from the reticulum and rumen through the omasum to the abomasum seems to be fairly regular throughout the twenty-four hours and the flow of food from the abomasum to the duodenum is also fairly regular suggests that the apparently continuous secretion of gastric juice in the abomasum is related to the continuous passage of food through the organ Considerable fluctuation of acid secretion by innervated fundic pouches of the abomasum have however, been noted by Hill (1955) and Ash (1959) which has led to research in order

to study the factors regulating secretion and recent papers by Hill (1960) and Ash (1961) provide convincing evidence that the secretion of acid by the fundic glands is integrated with the passage of omasal contents into the abomasum and of abomasal contents to the duodenum.

Emptying and rinsing the cavities of the reticulum and rumen free of food reduces or abolishes the secretion of acid by the abomasum (Hill, 1955). Infusing rumen liquor into the abomasum, however, causes a copious secretion of gastric juice by innervated fundic pouches. Further analysis (Ash, 1961) has shown that distension of the abomasum by saline-filled balloons or by saline solution stimulates secretion and the introduction of phosphate buffers with and without fatty acids stimulate secretion but secretion is greater when fatty acids are present. Secretion under these circumstances proceeds until the pH of the abomasal contents is reduced to between pH 1·9 and 2·8 when inhibition occurs. Inhibition in these experiments was not the result of acid material passing to the duodenum as this was prevented by using sheep with an exteriorized flow to the duodenum. Also, the introduction of phosphate fatty acid buffers into the abomasum at pH 2·1–2·4 failed to stimulate secretion. The introduction of acidic solution (pH 2·2 or thereabouts) into the duodenum inhibited the stimulatory effect of introducing rumen contents or fatty acid phosphate buffers into the abomasum.

These experiments suggest that the volume of contents entering the abomasum and its fatty content are important in stimulating acid secretion; and that acid secretion is inhibited when the contents of the abomasum is sufficiently acidic. Ash (1961) concludes that acid secretion by the abomasum can be controlled adequately by the conditions within the abomasum although noting that the experiments do not preclude the possible significance of effects from the duodenum and possibly the forestomach.

ABOMASAL DIGESTION

The weight of the contents of the abomasum of sheep fed dry rations every 12 hours increases from the second to the fourth hour after feeding although the dry-matter content shows little change, so that the total content of dry matter according to the figures of Boyne *et al.* (1956) has about doubled. The abomasal juice contains pepsin which is secreted continuously and the concentration of pepsin in juice secreted from innervated pouches does not seem to vary very much (Hill, 1961). The digestive activity of the juice, as in other animals, is on proteins but the acidity of the juice also has the important property of killing at

least a large proportion of the organisms that enter the abomasum Protozoa are very susceptible to acidic conditions and it is easy to see under the microscope that they are in an advanced state of disintegration in the abomasal contents Many of the bacterial cells lose their definition and staining properties and certain organisms such as Oscillospira show a degree of disorganisation (Smiles and Dobson 1955) It is wrong, however, to suppose that the abomasal contents are sterile, for it is possible to isolate bacteria from them but the concentrations are small compared to those found in the rumen

INTESTINAL DIGESTION

As far as is known digestion in the intestines of ruminants is essentially the same as it is in other animals Owing, however, to the system present in the stomach, quantitative differences are likely when comparison is made to animals with a simple stomach Thus the volume of pancreatic juice secreted and the responses elicited by secretion and other stimuli are usually smaller than those found in the dog (Hill 1961, Magee, 1961) The rate of secretion in feeding is given as 0 3–0 7 ml /kg /hr by Taylor (1958), secretion was at its lowest level between 4 p m and 10 p m but was almost constant during the remainder of the day Continuous secretion depended upon the food present in the alimentary tract as emptying the rumen reduced secretion to negligible proportions Pancreatic juice contains a concentration of amylase similar to that of the dog but as the volume of juice secreted is less, this enzyme is secreted in smaller quantity (Hill, 1961) Fermentation of carbohydrates in the rumen means that very little soluble polysaccharides—apart from those present in protozoan and bacterial cells—enter the intestines when animals are fed on grass or other fodders, or on roots Protein digestion seems to be the most important function of the intestines and Hogan (1957*a* *b*) (Table 7 3) has made estimates of the extent of the digestion of carbohydrate and of nitrogen-containing substances that go some way to support this

TABLE 7.3 *Proportional losses of the total dry matter and nitrogen between the food and the faeces of sheep fed on 300 gm hay and 200 gm concentrates every 12 hours (from Hogan, 1957a)*

	per cent of total loss	
	Dry matter	Total nitrogen
Stomach	70	36
Small intestine	10	61
Large intestine	20	2

generalization. It is possible, however, the food will influence considerably the quantities of its constituents that enter the small intestines intact. The modern tendency to feed animals largely on cereal grains and other concentrated foodstuffs and to reduce severely or even omit roughages from the ration may produce quite a different picture.

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CHAPTER EIGHT

The Measurement of Pasture Output

W. F. RAYMOND

Introduction—Measurement of pasture: herbage nutritive value, estimation of herbage intake—Measurement in terms of animal production.

The evaluation of pastures has received little attention compared with that paid to concentrate feeds, a position which has arisen from the traditional view of herbage as a roughage feed. However, the work of Woodman, of Newlander and Jones, and of Watson in the 1930s, which demonstrated that well-managed grass can be a highly digestible feed of high crude protein content, coupled with the pioneer studies of pasture improvement by Stapledon and his colleagues at the Welsh Plant Breeding Station, led to a realization of the high potential of herbage in animal production. This new attitude received impetus from wartime and post-war shortages of concentrate feeds; and, from an apparently minor position, grassland has now assumed an importance in world agriculture reflected by the major research effort being devoted to it. Besides its importance as livestock feed, the value of grass in maintaining soil fertility and combating erosion has led to much pasture research in areas in which grain was previously the principal crop.

Until recently, however, the main emphasis in this research was on the breeding of improved herbage varieties, on seeds mixtures and pasture establishment, and on pasture ecology, rather than on the evaluation of grass as a feed for ruminants—a position clearly reflected in the high proportion of papers on these subjects which were presented to the 6th (1952) and 7th (1956) International Grassland Congresses. This resulted partly from the first importance of knowing

how to increase herbage production, but also because of the particular difficulties involved in measuring pasture output and nutritive value. Much work on these latter aspects is now in progress, and is discussed in the present chapter. No really adequate methods of pasture evaluation, however, are yet available.

Pasture is growing and changing in composition during many months of the year, its composition and nutritive value depend largely on its constituent herbage species and on its management and manuring. It is also subject to more or less selective grazing by different classes of grazing stock. This means that the amount and quality of the herbage eaten is continually changing. Thus, grazing must be looked on as a dynamic process, compared with the less variable intake of stall-fed animals, and this presents the main problem in adequate pasture evaluation.

Pasture output can be expressed either in terms of the quantity and quality of the herbage grazed, or in terms of the output of animal products, and these will be discussed in turn. It is clear, however, that our understanding of pasture evaluation will be incomplete until we can equate these two measures of output.

MEASUREMENTS OF THE PASTURE

The consumption of nutrients from pasture is the product of the nutritive value per pound of herbage multiplied by the number of pounds of herbage consumed.

HERBAGE NUTRITIVE VALUE

Earlier nutritional studies established that herbage is of highest digestibility when it is at an immature growth stage, and that its digestibility decreases as it becomes more mature and stemmy. These changes are accompanied by changes in chemical composition, of which a decreasing crude protein content is frequently the most marked. Because of this association, the crude protein (C.P.) content of herbage gradually came to be taken as the main index of the value of herbage, not only as a protein feed, but also as an energy (starch equivalent) feed. In fact the quantitative evidence for this conclusion was slight, being based mainly on a study by Watson and Horton (1936) of the starch equivalents of herbages from a limited range of seeds leys. From these they derived the relationship

Starch equivalent = 0.689 × % crude protein in herbage + 47.97 [1]

They emphasized that this equation should be applied only to herbages closely resembling those studied, but despite this qualification 'Watson's regression equation' has been widely used to estimate the starch equivalent of all types of herbage in grassland experiments. A recent study of digestibility data from over 400 herbages fed at the Grassland Research Institute has shown a very low correlation between herbage digestibility and C.P. content ($r=0{\cdot}48$). Furthermore, a marked seasonal trend was found (Minson and Kemp, 1961) a given C.P. content in herbage representing a progressively decreasing digestibility from spring to autumn. Inter-species bias also occurs, so that the digestibility of lucerne is markedly lower than that of grass of the same C.P. content.

These results clearly indicate the limited value of crude protein as an index of herbage digestibility, and emphasize the importance of investigations on other herbage components. Of these some measure of fibre content has appeared most promising, and two of the first relationships were those proposed by Lancaster (1944) and Hallsworth (1949) respectively:

$$\text{Organic matter digestibility} = 94{\cdot}04 - 2{\cdot}95 \times \%\ \text{lignin in herbage} \quad [2]$$

$$\text{Starch equivalent} = 95{\cdot}11 - 1{\cdot}633 \times \%\ \text{crude fibre in herbage} \quad [3]$$

More recently Kivimäe (1960) has published relationships between the digestibility and the crude fibre, lignin, methoxyl and crude protein contents of 58 herbages. The regressions were found to differ between timothy and red clover, and also between different cuts of the same species. These results have helped to confirm the conclusion that chemical composition *per se* is most unlikely to give an accurate prediction of herbage digestibility. It appears that physical characteristics of the herbage, and in particular the way in which the fibre is organized, have an appreciable effect on the extent of digestion of this fibre by the ruminant. Thus two herbages containing the same (chemical) fibre contents may be digested to different extents because they have different physical structures.

To overcome this difficulty various workers have investigated a biological method (the so-called *in vitro* or 'artificial rumen' technique) which attempts to simulate bacterial digestion in the rumen, and so takes account of both the chemical and the physical characteristics of herbage. This technique has proved of real value with low-protein feeds, but with feeds high in protein content it has frequently given digestibility results much lower than those *in vivo*.

Tilley *et al* (1960) suggested that this might be due to the fact that the 'artificial rumen' techniques which had been used involved only digestion with rumen organisms, whilst *in vivo* digestion involves both bacterial digestion in the rumen and enzymic digestion in the hind-tract They suggested that incubation of the sample with rumen organisms should be followed by treatment of the residue with acid pepsin With this technique they obtained remarkably close agreement between *in vivo* and *in vitro* digestibility estimates with herbage feeds ranging in digestibility from below 45 per cent to over 80 per cent, and varying markedly in C P contents This two-stage *in vitro* method appears the most promising laboratory method to date for estimating herbage digestibility it has the particular advantage that it requires only small amounts of herbage (2×0 5 gm dry matter) and so can be applied to different chemical or botanical fractions of herbage plants Thus it has been possible to show that, as the lucerne plant matures, the digestibility of the leaf remains almost constant, whilst that of the stem decreases markedly this indicates that the level of digestibility of the lucerne plant is determined almost wholly by the proportion and digestibility of the stem fraction (Grassland Research Institute, 1961*a*)

These observations illustrate one of the main difficulties in applying indoor digestibility data, whether from *in vivo* or *in vitro* experiments, to the estimation of the digestibility of herbage as grazed This arises from the selective nature of grazing by stock. Clearly the digestibility of grazed lucerne must depend very much on the proportion of leaf to stem which the grazing animal selects, these in turn will depend on the stage of maturity of the crop, and on the intensity of utilization, which determines the proportion of the total crop that the grazing animals will consume Similar differences in digestibility, though seldom so marked, appear to occur between the leaves and stems of all herbage species, and also between the different herbage species growing together in a mixed sward. Thus any differential grazing, either of one portion of a herbage plant, or of one species from a mixed sward must lead to an intake qualitatively different from that of the whole sward, which would be sampled for laboratory analysis As stock generally select the leafier and more digestible components of a sward, neglect of the selective grazing factor may lead to an underestimate in herbage digestibility, and this factor must be accounted for if reliable pasture data are required It has been suggested that, by close observation of the grazing animal, it should be possible to pluck a sample of

herbage representative of that grazed, but Saltonstall (1948) has shown, by collecting 'herbage eaten' through a rumen fistula, that it is most difficult to simulate selective grazing by the cow. The problem would be even more acute with sheep, which tend to be more highly selective than cattle. However, the development of the oesophageal fistula (Torell, 1954), allows the collection from the animal of the portion of the 'herbage grazed', and determination of the *in vitro* digestibility of this sample may allow a reasonable estimate to be made of the digestibility of the herbage grazed.

An alternative approach, the faecal index method, is based only on chemical analysis of the faeces from grazing stock; it assumes that, if a relationship between herbage digestibility and faecal composition can be established from indoor-feeding data on a range of herbages, then use of this relationship in the field should allow the prediction of the digestibility of 'herbage grazed' from an analysis of the faeces produced by the grazing animals. A relationship between the nitrogen contents of herbage feeds and of the resulting faeces samples was noted by Raymond (1948):

$$\%\ \text{N in feed} = 0{\cdot}795 \times \%\ \text{N in ash-free faeces} + 0{\cdot}14 \qquad [4]$$

and it was suggested that the N content of faeces could be used as a measure of the type and quality of herbage being grazed in the field. Quite independently Lancaster (1949) showed a relationship between herbage digestibility and the nitrogen content in faeces:

% digestibility of herbage organic matter=

$$\% \text{ digestibility of herbage organic matter} = 124\ 22 - 1\ 058Y \quad [7]$$

$$(r = -0\ 93)$$

(where Y= per cent normal-acid fibre in faeces organic matter normal acid fibre is the organic residue from a 1-hr digestion with N sulphuric acid of alcohol/benzene extracted faeces)

These and similar relationships have been widely used in grazing experiments, but sufficient attention has not always been paid to the errors likely in their use Thus these relationships have often been used without due regard to their associated prediction errors, which have been large enough to make calculated differences in digestibility between feeds non-significant Furthermore these errors are frequently biased, rather than random, as is assumed in regression theory, and are likely to lead to biased estimates of digestibility Thus a study of the errors in herbage digestibility/faecal N relationships has shown that data for spring herbages are consistently above the mean (all-seasons) regression, whilst data for autumn herbages are below the line This means that use of the mean line must underestimate the digestibility of herbages grazed in the spring and overestimate that of herbages grazed in the autumn (Greenhalgh *et al*, 1960, Minson and Kemp, 1961) This must lead to faulty interpretation in long-term grazing experiments It further explains some of the differences which have been noted between the faecal index regression equations produced by different workers, as clearly the mean regression line obtained by any one worker will depend largely on the between-seasons distribution of the herbages on which it was based Two methods of overcoming this problem have been proposed 'local regression' and 'correction' methods (see Grassland Research Institute 1961*b*) In both of these, digestibility determinations must be made on herbage cut from the swards being studied, the use of the faecal-index method without such associated digestibility measurements is likely to give invalid results

A further source of error arises from the use, in the field, of relationships based on indoor feeding experiments The most serious of these results from the different level of intake in indoor experiments from that at grazing It has been shown (Raymond *et al*, 1956) that this is likely to lead to incorrect estimates of the digestibility of 'herbage grazed' when regressions based on normal-acid fibre or lignin contents of faeces are used Even with faecal nitrogen it appears advisable to

subtract 1·5 units from the estimated digestibility to allow for this factor (Grassland Research Institute, 1961*b*).

Furthermore, there may be differences between the regressions for cattle and those for sheep, and where possible the indoor and the field experiments should be based on the same class of stock.

It is thus clear that considerable care is needed in the use of the faecal-index method if valid results are to be obtained, and this must restrict its practical application in grazing experiments, until more precise relationships are developed. However, it can provide interesting qualitative evidence, especially on the effect of management on the type of herbage selected in the field (see e.g. Blaser *et al.*, 1960). Thus in an experiment (unpublished) at the Grassland Research Institute, two groups, one of twelve and the other of six sheep, were rotationally grazed throughout the summer on two similar sets of four quarter-acre paddocks. With each group the high-digestibility herbage available for grazing on entry into a fresh paddock was reflected in a sharp rise in the nitrogen (C.P.) and chromogen contents in the faeces produced on the following day. The fall-off in the digestibility of the herbage eaten as grazing proceeded was indicated by the decreasing N and chromogen contents in the faeces on succeeding days. In the case of the group of 12 sheep however these changes in composition were more marked than with the 6 sheep, indicating, as might be expected, that they were removing the more digestible parts of the sward more rapidly: also because of the higher level of stocking they were obliged to utilize the herbage available more completely, so that the herbage they consumed was on average of lower digestibility (Fig. 8.1). As a result of this differential management they made an average live weight gain from May to October of 54 lb. only, compared with 64 lb. gained by the more lightly stocked group. Although reduced feed intake by the larger group must have accounted for part of this difference, the poorer quality of the feed eaten, as reflected by faecal compositions, may well have been an important factor: the relative importance of quantity and quality of feed intake requires much further study. This experiment illustrates the application of the faecal-index method in detecting quite small differences in the quality of day-to-day herbage intake from a given sward, which would not be possible by any other method yet developed.

Although it may give useful information on the digestibility of the herbage being grazed, the faecal-index method can give no indication of the botanical composition of this herbage. An interesting method

developed for use with the very mixed flora of hill grazing (where knowledge of the botanical composition of the herbage grazed is of much importance) was first described by Martin (1955). Microscope sections are made of all the plant species likely to be grazed in the area being studied. Faeces from the grazing stock are also examined microscopically, and details of the fragments of plant cuticle in the faeces are compared with those of the control plant sections. This technique has since been used by Hercus (1960) in New Zealand, and this author

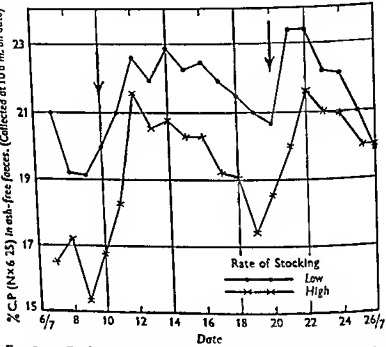

FIG. 8 1. Crude protein content of faeces from sheep rotationally grazed at high or low levels of stocking Stock moved to new paddocks at 10.30 a m. on days indicated by arrows.

suggested possible quantitative developments of the method. However, with certain plant species, the cuticle appears to be completely destroyed during digestion and examination may then have to be made on samples withdrawn from the rumen. An alternative method is the use of the oesophageal fistula, which by-passes the feed eaten into a collection bag under the neck: this sample can then be examined for botanical makeup, which is relatively simple, as the herbage has not been broken down by rumination and digestion.

Botanical information on grazing intake can also be obtained by the 'browse unit' method of Cook *et al.* (1948), in which samples of the

plant species available are taken before and after grazing. This method is particularly applicable to range grazing, where different species frequently form discrete colonies. A combination of the microscopic and 'browse unit' methods would be of much interest.

Herbage nutritive value has so far been discussed in terms of digestibility, but it is not certain how closely digestibility data are a reflection of the true productive value of a herbage feed. However, recent energy metabolism experiments at the Hannah Dairy Research Institute (Blaxter, 1960; Armstrong, 1960) have indicated a close relationship between herbage digestibility and net energy values, although as herbage digestibility decreases net energy for animal production falls off more rapidly than digestibility. This appears to be related to the different proportions of volatile fatty acids produced during the digestion of different herbages in the rumen. These data indicate that acetic acid is less efficiently utilized as a source of energy for lipogenesis than are propionic or butyric acids; thus the higher proportions of acetic acid and the lower proportions of propionic acid and butyric acids in the rumen liquor of sheep fed on mature ryegrass compared with those fed on young ryegrass may explain the more efficient utilization of the 'digested' energy in the latter. For milk production the individual fatty acids appear to have specific functions; thus acetic acid is a precursor of milk fat (Folley, 1956) and propionic acid appears to be involved in milk solids synthesis (Kleiber *et al.*, 1953; Rook, 1959). Balch (1960) has also shown that acetic acid is more efficiently used for total milk production than is propionic acid. Thus it appears that the optimum rumen volatile fatty-acid pattern for milk production will differ from that for fattening, and that the acids produced by rumen fermentation of a given herbage will be more suitable for one class of production than for the other. If these concepts are confirmed, it may mean that a combination of an *in vitro* measurement of herbage digestibility, together with an *in vivo* measurement of the proportions of volatile acids in the rumen of an animal on the same feed, may give a useful measure of the value of that herbage for different types of animal production. A further advance would be a laboratory method of predicting rumen acid proportions, and this merits careful study. Elucidation of both the energetic and synthetic requirements of the animal should allow a more rational understanding of the relationships between herbage digestion products and their value to the ruminant, and should in turn allow a better definition of herbage nutritive value.

Herbage must supply the requirements of the ruminant for energy and protein, as well as for essential minerals In addition it should not produce metabolic or physiological disorders (the main subject-matter of the present volume) and it must be palatable Despite a suggestion to the contrary (Blaxter *et al*, 1961) it seems clear that palatability has real meaning with herbage feeds, i e that certain herbages are intrinsically more acceptable to livestock than others Undoubtedly, digestibility has a dominant effect on intake (Crampton *et al*, 1960, Blaxter *et al*, 1961), in that animals tend to eat most of those herbages which are of highest digestibility However, herbage intake experiments carried out under *ad lib* feeding conditions at the Grassland Research Institute have shown marked differences in intake between different herbage species when at the same digestibility This is likely to be due in part to differences in *rate*, as opposed to *extent*, of digestion (Crampton *et al*, 1960), but differences in acceptability are most evident Thus fouling with excreta or soil fungal infections on pasture, mould in hay, excessive moisture in silage, all seem to reduce acceptability It appears essential to consider those attributes of herbage which affect intake, as well as its content of digestible energy, protein and minerals, in defining its quality as a ruminant feed

THE ESTIMATION OF HERBAGE INTAKE

Various techniques of estimating pasture production have been proposed, but only those which are relevant to actual grazing conditions will be considered here—thus the alternate grazing and mowing technique (Hudson, 1933) gives an estimate of pasture output under a mowing technique in which the animals are used to ensure return of excreta to the pasture A full review of pasture evaluation techniques has been given by Brown (1954)

The most commonly used technique for estimating the consumption of pasturage is the 'difference' method, the weight of herbage on the sward is estimated by sampling before and after grazing and the difference is taken as the weight of herbage consumed However, this neglects the growth of herbage on the sward during the grazing period. To allow for herbage growth areas of the ungrazed sward may be protected by cages, intake being the difference in yields between 'caged' and 'grazed' areas sampled at the end of the grazing period In this case an overestimate of intake is likely, since the herbage in the 'caged' areas will have grown more than the partially defoliated herbage on the grazed sward, the protection of the 'cage'

may also set up a microclimate more favourable to growth than the open sward (Cowlishaw, 1951). To overcome the former objection Linehan *et al.* (1947) and Lowe (1959) proposed a relationship:

$$\text{amount of herbage consumed} = (c-f)\cdot\frac{\log d - \log f}{\log c - \log f} \qquad [8]$$

in which c = herbage on sward before grazing
d = herbage in 'caged' area after grazing
f = herbage on sward after grazing

However, the assumptions on which equation [8] is based do not appear to be exact (i.e. neither rate of consumption nor rate of herbage growth is likely to be proportional to the amount of herbage on the sward at a given time), and the estimation of herbage intake as $[(c+d)/2-f]$ would seem as reasonable an estimate as can be made at present with the mowing technique.

A further error, which has seldom been noted, is that most cutting implements used in grazing experiments cut at a height above the level to which stock may graze down the sward. This is most serious when little herbage is available or intensity of stocking is high, but even with plenty of herbage on offer stock often graze some areas of the sward close to the ground. If herbage is grazed from below the level at which samples are cut an underestimate of consumption must result. Neglect of the two factors of differential growth between 'caged' and 'grazed' areas, and of the effect of close grazing must invalidate the results of many of the cutting experiments that have been carried out. Unfortunately this has frequently not been apparent from published results, because of the presentation of 'yield' as a cumulative figure, which has frequently shown reasonable agreement with estimates from animal production data. An analysis of data for the individual grazing periods shows that, early in the grazing season, consumption of herbage is generally overestimated, owing to the differential growth error, and later in the season consumption is underestimated because stock are grazing increasingly below cutting level. That the cumulative figure for the grazing season may appear reasonable is thus quite fortuitous, since it is the sum of over- and under-estimates of intake, which only chance to be equal (Fig. 8.2). This was demonstrated in an experiment (unpublished) in which the herbage consumption of sheep under rotational grazing was estimated on each paddock by (1) the difference method $(d)-(f)$, using a mower cutting at 1–1½ ins.,

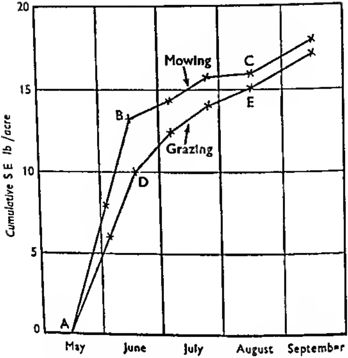

FIG 8 2 Comparison of output from a pasture estimated from either grazing or mowing techniques

and (2) a faecal collection method (see below) The ratio 1 2 for each grazing period was plotted against the amount of herbage available (*d*) and gave the relationship in Fig 8 3 The difference method gave a higher estimate of consumption than the faecal method when much herbage was available, but a considerably lower estimate when little feed was available (in one grazing period *faecal* dry-matter production was three times the estimated herbage intake) Except when herbage is long and grazing intensity low it seems essential to sample the sward close to ground level, either with hand shears, or with some type of power-operated clipper, a sheep-shearer with special head has proved most suitable (see Grassland Research Institute, 1961*b*)

A further difficulty with cutting techniques arises from the errors associated with sampling the herbage on the sward On a fresh ungrazed pasture in the spring these errors may be reasonably low, but as the season proceeds pastures become less uniform owing to uneven grazing, particularly around soiled areas, and the number of samples required to obtain a satisfactory estimate increases The 'difference method' requires estimates to be made of the herbage on 'grazed' and 'caged' areas, so that the errors of both are combined in the estimate of

'herbage grazed'. Green (1952) has shown that to reduce to below 5 per cent the error of an estimated 1,000 lb. D.M., removed during one spell of grazing, may require as many as 100 pairs of samples (6 ft. × 1 ft.), and this seems impracticable in any but the most critical experiments. This source of error is most important when estimates of consumption under continuous grazing are being made. In this case the difference between the herbage cuts on the 'caged' and 'grazed' areas is likely to be much smaller than during a corresponding period on a rotationally grazed plot, with a proportionately higher standard error of estimate of the difference.

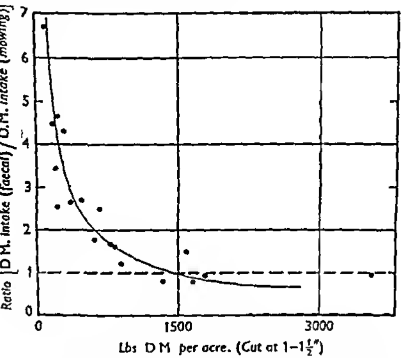

FIG. 8.3. Comparison of two methods of estimating dry-matter intake by grazing sheep (mowing and faecal collection methods) at different levels of available herbage.

Except under 'strip' grazing, when an estimate of daily intake can be made (e.g. Holmes *et al.*, 1950; Van der Kley, 1956) mowing techniques are also unlikely to give adequate estimates of day-to-day changes in amount of intake. These, together with changes in quality of intake, are of particular importance on rotational grazing, as can be seen by the trends in milk production from a dairy herd grazed under this system.

In many experiments chemical analyses, especially for C.P. content, have been made on 'caged' and 'grazed' samples, and the content of

C P in the 'herbage consumed' has been calculated from these analyses, together with the dry-matter contents of the cuts Such estimates have generally shown the quality of 'herbage grazed' to be better than that of 'caged' cuts—which would be expected as a result of selective grazing by stock—but they are sensitive both to the errors in cutting techniques already discussed and to further sampling and analytical errors In some experiments the digestibility or starch equivalent of the herbage grazed has been calculated from this estimate of C P content, but this appears an invalid procedure

An alternative technique was described by Garrigus and Rusk (1935), and Woodman *et al* (1937) These workers determined the digestibility of the herbage cut from a sward which allowed an estimate of the quantity of faeces produced per pound of herbage consumed (both on a dry-matter basis) Stock, grazing herbage similar to that cut, were equipped with harness and bags which collected all their faeces These faeces were weighed and, from the relationship obtained in the indoor experiment, the quantity of herbage which must have been eaten to produce this weight of faeces was calculated this was taken as the weight of herbage grazed

Weight of herbage consumed=

$$\frac{\text{weight of faeces}}{100-\%\text{ digestibility of herbage}}\times 100 \qquad [9]$$

The technique in its original form has been used in relatively few experiments because of the labour required for total collection of faeces from numbers of animals as well as the need for associated digestibility experiments However, its main disadvantage, discussed by Woodman is the assumption that the digestibility of the herbage grazed in the field is the same as that determined on cut herbage in the indoor experiments Because of the selective grazing factor this will seldom be true, and the digestibility of 'herbage grazed' will be underestimated, leading to an underestimate of herbage consumption More recently a modification of the technique has been widely used, in this the digestibility of herbage grazed has been estimated from the chemical analysis of the faeces produced, using the faecal-index method, and the weight of faeces voided has been estimated by an *external* tracer technique This is based on a method originally used (1918) in indoor experiments (described by Edin *et al* 1944–5) If a known weight of

a 'tracer', which has been shown to be indigestible, is fed to an animal, the same weight will be excreted in the faeces. If the concentration of tracer present in a small sample of faeces is measured, the total weight of faeces voided can then be estimated:

$$\text{weight of faeces excreted (gm.)} = \frac{\text{weight of tracer fed}}{\text{weight of tracer per gramme of faeces}} \quad [10]$$

The accuracy of this technique depends on two assumptions, namely that the tracer is in fact completely indigestible, and that the sample of faeces analysed is truly representative of the whole excreta. Chromic oxide (Cr_2O_3) has been the most widely used tracer, being cheap and inert, and having given recoveries close to 100 per cent in many experiments with ruminants. Weighed quantities of this tracer are fed once or twice daily, either mixed with a supplementary grain feed, or in gelatin capsules administered with a balling gun. In order to produce a concentration of Cr_2O_3 in the faeces suitable for chemical analysis, 2 gm. per day are generally fed to sheep and 15–20 gm. per day to cattle. Dosing should start 7 days before the experiment commences to distribute the tracer throughout the feed in the tract.

In earlier indoor experiments the tracer was mixed with the whole feed, and so was distributed fairly uniformly in the faeces; as a result sampling of faeces presented no problem. It was not at first realized that in grazing experiments the tracer is *not* mixed uniformly with the feed, and so is excreted irregularly in the faeces. This makes careful sampling of faeces essential. Kane *et al.* (1952) showed a diurnal pattern of excretion of Cr_2O_3 in the faeces, and suggested that, from a knowledge of this pattern, it should be possible to predict sampling times at which faeces containing the true average concentration of oxide would be obtained. This method assumes that a pattern of diurnal excretion identical with that found in these controlled experiments will occur with other animals under other conditions of feeding. It has since been shown however that the excretion pattern, and in particular the times of maximum and minimum concentrations of Cr_2O_3 in the faeces, depend among other factors on the times and method of dosing in relation to the pattern and level of feed intake (Raymond and Minson, 1955). It appears that the higher the level of feed intake the more rapidly after dosing does the maximum concentration of Cr_2O_3 occur in the faeces, probably because of the higher rate of passage of feed

residues down the hind tract. As feed intake in the field is variable this must mean that no constant pattern of excretion of Cr_2O_3 occurs and that sampling of faeces at fixed times is an unreliable procedure.

Raymond and Minson (1955) suggested sampling faeces directly from the sward as an alternative method of obtaining a representative sample of faeces for analysis for Cr_2O_3. With sheep, faeces are completely cleared each day from fixed sampling areas on the sward, so that any faeces in the sample must have been excreted during the preceding 24 hours. In the case of cattle each 'pat' of faeces on the sward is subsampled, the 'pat' being sprinkled with powdered chalk to avoid sampling again on a later occasion. As all the faeces produced by the grazing stock are distributed on the sward it is evident that any required degree of precision can be obtained by sufficiently intensive sampling; errors arise mainly from very uneven distribution of excreta, as when stock congregate in shade during warm weather or near drinking troughs.

Two alternative methods of dosing Cr_2O_3 are being studied, with the object of reducing the magnitude of the variations in faecal Cr_2O_3 content, and so facilitating precise sampling of the faeces. The oxide is dosed either in slow-release capsules (Brisson, 1960) or incorporated in kraft paper (Corbett, 1960); both methods mix the oxide more uniformly with the feed in the rumen than is possible with normal capsule dosing. As a result the concentration of Cr_2O_3 in the faeces is much less variable, so that a less intensive sampling method is required.

With careful dosing with Cr_2O_3 and the appropriate sampling of faeces from the sward, an estimate of faecal production very close to that obtained by total collection in bags is possible. The technique is much less laborious than total collection, does not disturb the stock, and does not interfere with return of fertility to the sward, as does total removal of faeces. The total collection method has, however, permitted an estimate of the faecal production by each individual grazing animal in a group. In the case of cattle this is now possible by dosing each animal, at the same time as the Cr_2O_3 is dosed, with a capsule containing polystyrene particles of distinctive colour (Minson *et al.*, 1960). These pass largely undamaged into the faeces, and each 'pat' of faeces on the sward can be allocated to a particular grazing animal by the presence in it of plastic particles of the appropriate colour. The faeces from five individual animals or groups of animals grazing together have been readily distinguished in this way.

As noted above, the faecal-index method has been widely used for estimating the digestibility of herbage grazed (equation [9]), but again

the various errors associated with this technique have not always been taken into account in discussing the precision of the resulting intake figures. This is even more serious than appears at first, because of the term (100 – digestibility) in equation [9]. This will magnify the effect of errors in the estimation of digestibility: digestibility is generally between 60 and 80 per cent in the case of herbage feeds. It seems essential to take all the precautions noted above in the discussion of the faecal-index method; even so it seems unlikely that at present differences of less than 15 per cent in herbage intake between different swards can be detected with any degree of significance. Further improvement of the method is urgent, in terms both of simplicity and of precision, as the need increases for reliable intake data in pasture experiments.

MEASUREMENT IN TERMS OF ANIMAL PRODUCTION

Pasture production has so far been discussed in terms of the quantity and quality of herbage grazed. However, the most commonly used methods of evaluation depend on measurements of animal output from pasture; these are in general simpler to carry out than indirect techniques, and have appeared to be more closely related to the practical problems of pasture production. Two main problems arise in these evaluation systems based on animal data: first, in the accurate measurement of animal production at pasture; and second, in the interpretation of the results, which is frequently not as straightforward as has been assumed.

One system, used mainly in farm survey studies, evaluates pastures in terms of the number of grazing days, generally 'cow grazing days' which they provide. Tables have been produced suggesting figures for grazing days by other classes of stock in terms of the standard cow (see Brown, 1954). However, this method takes no account of the production by the grazing animals, which is likely to be different on different pastures. For this purpose systems have been developed which require more extensive recordings, including changes in animal liveweight, milk or wool production, and supplementary feeds given. These, together with grazing days, are brought together in terms of total digestible nutrients or starch equivalents, pasture output being computed as the animal requirements for maintenance plus production less the feed value of the supplementary feeds given (Barker *et al.*, 1955).

These recording methods have proved of most value in 'within-farm' studies, where variables such as class of stock, management

efficiency, levels of supplementary feeding etc are minimized. For the reasons discussed in more detail below they can, however, only measure the realized animal production from a pasture under the particular conditions imposed, and this may differ markedly from the potential animal output of that pasture. Thus, measured differences in animal output between pastures on one farm, and more particularly between pastures on different farms, frequently measure differences in efficiency of exploitation rather than differences between the potentials of the pastures as livestock feeds.

Output of animal products has also been used in pasture experiments, and in particular in comparisons of management systems or of sward types. For these comparisons animal data are converted to feed nutrient equivalents, but this procedure is uncertain, partly because of the likely variability in maintenance and production requirements between individual animals, which may introduce errors unless adequate numbers of animals are used in each group, and partly because these requirement-data have been obtained in indoor feeding experiments, and it is uncertain how far they are applicable to grazing animals (see N Z Soc Anim. Prod., 1961). Thus recent data indicate that the maintenance requirements of grazing stock may be higher than those of pen-fed animals (Lambourne, 1961). In relation to animal production, feeding standards generally imply a linear response between production and increments of feed input. In fact, as production increases, efficiency of conversion of feed nutrients appears to decrease. This means that the use of uniform feeding standards for animals varying widely in production levels is unsound. Furthermore, where supplementary feeds are given they are always allocated a production value based on these feeding standards, at high levels of production this must inevitably mean that the quantity of herbage nutrients required to give the remaining animal production will be underestimated, leading to an underestimate in the consumption of nutrients from the pasture. It is clear, therefore, that the conversion of animal output data from field experiments to nutrient intake data, using existing feeding standards is subject to considerable errors, and further work on more precise feeding standards under grazing conditions is required.

In such evaluation systems accurate measurement of animal production is also required and this can be most difficult under pasture conditions. Thus live weight increase measurements are sensitive to changes in animal 'fill', which can be very marked on pasture, where

the type and amount of herbage available vary widely. Fig. 8.4 shows the average live weight of a group of 12 sheep, weighed daily while under rotational grazing (Raymond, 1957). Movement of the sheep to a fresh paddock was followed by a sharp rise in live weight on the following morning, and live weight was then found to decrease gradually as the paddock was grazed down, rising again after movement to a further paddock. It is evident that, although the general trend in

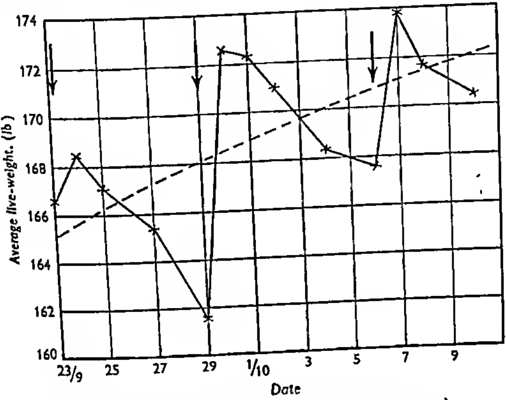

FIG. 8.4. Average live weight (10 a.m.) of 12 sheep on rotational grazing Stock moved to new paddock at 10.30 a.m. on days indicated by arrows. Dotted line shows general live-weight trend

live weight could be followed, no accurate measurement of gain resulting from grazing on a single paddock was possible. These fluctuations in live weight are not as marked under either set-stocking or strip-grazing conditions, but changes in 'fill' over a period may still be of the same order of magnitude as true live-weight gain. Thus, when cattle from yards are turned out to pasture, losses in live weight of up to 50 lb. may be recorded within a few days; this has been shown to be almost entirely due to reduction in 'fill', and, unless allowance is made for this, incorrect live-weight gain data will be recorded during subsequent grazing periods (Tayler *et al.*, 1957).

In order to reduce variations in 'fill' it has been suggested that

animals should either be weighed on successive days, and the average weights used, or else be fasted overnight to bring them to more standard conditions of 'fill' Both these methods are undoubtedly useful, but average weighings cannot compensate for a trend in 'fill' over a period, and fasting may be undesirable in many experiments, especially with dairy cattle In an alternative technique used by Kidder (1946), the rate of stocking and the time the stock are allowed to graze on a pasture are adjusted so that the animals neither gain nor lose weight, and are thus assumed to be consuming their maintenance requirements only This technique requires considerable skill in stock management and can of course give no evidence of the production potential of pastures, there is also the possibility that a true increase in weight may be concealed by a corresponding loss in 'fill', nor can changes in body composition be assessed

Measurement of milk production by dairy cattle is much more precise, but in early lactation it is not always certain that the milk produced is in direct response to intake of pasture nutrients, as the cow appears able to draw on body reserves for milk production at this time However, later in lactation, milk production appears more closely related to the quality and quantity of pasture intake, thus Jarrige and Journet (1959) found marked changes in milk production and composition as dairy cattle were moved from pasture to pasture—changes which appear to have reflected the quality of the different pastures Dairy cattle also present difficulties in the measurement of live-weight changes, similar to those met with growing stock, but the errors introduced are less serious, because most of their productive output is as milk, which is more accurately measured.

However, it is in the interpretation of animal output data at pasture that the main problem appears to arise This problem was posed by McMeekan (1956), in discussing an experimental comparison of set-stocking and rotational grazing, he showed that the result was very largely determined by the level of stocking (i e number of animals per acre) used in each treatment Thus, in some previous comparisons an increased output under rotational grazing had been assured by the subjective judgement that the rotationally grazed paddocks could be more heavily stocked than the set-stocked paddocks This situation was developed by Ivins *et al* (1958), in terms of 'animal' and 'pasture' potentials Under most conditions the potential of the pasture for animal production will either be greater than that of the grazing animals to exploit it, or less It is only in the latter case that pasture potential is

being measured; where pasture potential is greater than animal potential, animal output is entirely a function of animal potential × number of animals. It appears that, in many grazing experiments, animal potential is below pasture potential, because the animals are either too low-producing to exploit a high-quality pasture, or because there are too few of them to make full use of the herbage available. In either case the measure 'pasture output' is a function of the number and productivity of the animals used. Under these conditions the results obtained in pasture comparisons are clearly a reflection of subjective judgement of stocking rates, rather than of true differences in pasture potential. McMeekan (1956) suggested that, although output of animal products per acre increases with increase in stocking rate, it will not increase at the same rate because output per animal tends to decrease. At some point a further increase in stocking rate is exactly compensated by a decreased yield per animal; beyond this point more intensive stocking must lead to decreased output per acre. This point is effectively the maximum potential of the pasture, with the class of stock and management employed, and its determination requires a study of the interactions between level of stocking, output per animal and output per acre. Later results reported by McMeekan (1960) showed in fact that, although at medium levels of stocking, set-stocking and rotational grazing gave very similar outputs per animal, as the level of stocking was increased output per animal fell more rapidly under set-stocking than under rotational grazing. This meant that maximum animal output per acre was lower under set-stocking. This conclusion had been predicted on the basis of herbage-cutting experiments, but it was only confirmed by showing that, under set-stocking, pasture potential fell below animal potential at a lower rate of stocking than it did under rotational grazing. Clearly the same considerations must apply in making comparisons between pastures; unless several different levels of stocking are imposed on each pasture the results may be entirely due to subjective judgement of the appropriate rates of stocking to apply to the pastures (unless one of these is such that the animal potential applied is already greater than the pasture potential). Some of the practical implications of these conclusions have been discussed by Mott (1960); as pasture potential can vary more rapidly than animal potential (per animal), it may be necessary to adjust stocking rate fairly frequently to maintain a given relationship between animal and pasture potentials, i.e. it may be incorrect to impose a fixed rate of stocking on a pasture whose productivity can vary markedly at

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different seasons This again introduces subjective judgement, either in changing the numbers of stock, or possibly in allocating areas of excess herbage growth for conservation

At present, then, the results of grazing experiments, even when carried out at several rates of stocking, are still subject in a considerable degree to skill in pasture management What appears most necessary is quantitative information on the interrelations between type of pasture, management, level of stocking and output per animal, and here the methods of estimating pasture intake and nutritive value discussed in the first section are likely to be of most value Pasture output experiments, even when well carried out, can only show that differences in production exist, but can seldom explain why they have occurred, there is then little basis for predicting what would happen under another set of conditions By relating animal output to herbage intake and quality it should be possible to understand better the reasons for differences in animal output, and so to learn more about the basic principles of animal production from pasture

This discussion of pasture evaluation may seem out of place in a volume devoted mainly to animal health, but in fact it is probable that inadequate gross nutrient intake (energy plus protein) is one of the commonest causes of ill-health among animals at pasture Low intake may be accentuated or caused (as in the case of cobalt) by mineral deficiency, but it does seem that, when nutritional deficiency is suspected, the gross feed intake should first be investigated Lowered resistance to parasitic infestation may also be associated with inadequate food intake Thus accurate methods of measuring the herbage consumed by grazing stock are an integral part of the overall study of the health of the grazing animal, at present, knowledge of intake appears to lag seriously behind our knowledge of many of the other factors concerned in animal health, and this deficiency must soon be remedied if maximum production is to be obtained from pasture

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CHAPTER NINE

Grazing Behaviour

R. WAITE

The general pattern of grazing behaviour—Factors which influence grazing behaviour: climate and weather, individuality of grazing animals, quality and quantity of herbage, palatability, selection by animal, senses used, effect of feed supplements—Conclusion.

During the last 10–15 years the need to utilize grassland more efficiently has led to increased interest in the behaviour of the grazing animal. This has come at a time when the potentialities of grass as a farm crop are being more generally recognized and newer types of grazing management for cattle, such as close-folding and rotational grazing, have been introduced and accepted.

A study of animals at pasture, however interesting, must at best be only complementary to a wider study which would include the amount and digestibility of the herbage that is eaten during such grazing and, most important of all, what use the animal makes of these feeds for growth, maintenance and the production of milk, beef or wool. This type of work therefore involves a considerable number of people of differing skills over long periods and it is not altogether surprising that a fair proportion of the work concerned with grazing behaviour falls short of providing the maximum information that was possible. There are other limitations common to most reports to which the attention of the general reader must also be drawn. There has in the past often been an absence of close definition of the grazing conditions and even a lack of a common terminology which makes comparison of the results obtained by the various workers difficult. Although most workers are themselves well aware that records relating to only a few animals cannot necessarily be applied to the same class of animal in general,

nevertheless, the resources needed to study the individual performance of large numbers of animals are usually beyond those available. These are some of the caveats that need to be entered before discussing the absorbing problems of the grazing behaviour of our domesticated livestock and trying to interpret the results.

THE GENERAL PATTERN OF GRAZING BEHAVIOUR

Most observations of grazing behaviour record the time the animal spends in grazing and ruminating, and many give some indication of the time spent in lying down and in standing or walking without actually grazing. Periods of rest are taken as the time spent lying down without ruminating, and the periods when the animal is standing or walking about without either grazing or ruminating are taken as idling time. Other activities often recorded are the number of defaecations, urinations and drinks and, less frequently, the rates of grazing and ruminating, but for the purposes of animal production and pasture management, grazing and ruminating times provide the most important information.

Such records for cattle and sheep, made under a variety of conditions in a number of countries, vary in detail but show considerable similarity in the general pattern of grazing behaviour. In temperate climates most of the grazing by cattle is done in two periods during the daylight hours, the first commencing soon after dawn and the second starting in the early evening and going on until about one hour after sunset. For dairy cows the early morning grazing may be interrupted or postponed by milking and the start of the evening grazing period is again governed by their return from milking. About half the total amount of grazing is done between the evening and morning milkings, an observation of importance in those systems of management which employ night paddocks close to the milking quarters. Between the two long periods of grazing there are usually three or four shorter spells of rather more desultory grazing and about 80–90 per cent of the total period spent in grazing occurs during daylight. In hot climates this pattern is reversed and as much as two-thirds of the grazing is done in the cooler hours of darkness.

mid-morning are therefore usually spent in this way, and most of this rumination is done while the animals are lying down. The intensity of both grazing and rumination is greatest at the start of each period and rumination at night is frequently alternated with short periods of rest.

A similar pattern of alternating periods of grazing and ruminating is followed by sheep, although the amount of time spent in the first and last daylight grazing periods is shorter, making all the grazing periods of more equal length. Like cattle, sheep appear to graze very little in the dark in cool climates.

The part that sleep plays in the life of the ruminant has received little mention in the literature of animal behaviour probably because as several watchers have noticed, sound sleep, where consciousness is lost, appears to be unusual. During periods when the cow is lying on the ground the head is sometimes rested on the flank for short periods, often with the eyes closed, but the slightest extraneous noise or movement evokes an immediate response. Only rarely are adult cattle seen at rest lying flat on their sides and Balch (1955) considers that this is because the large volume of digesta in the rumen would thereby be displaced and lead to dysfunction of the reticulo-rumen. This need to keep the thorax in an upright position and the requirement of consciousness for rumination may therefore account for the absence of sleeping periods.

In Table 9.1 some of the recorded values for the grazing and ruminating times of different classes of animals are given and, as would be expected, they show considerable variation between individuals of the same species and, to some extent, between sheep and cattle. There are insufficient results from which to draw any firm conclusions but it would appear that, in each 24 hours, sheep graze somewhat longer than cattle and also probably ruminate longer, although the difficulty of observing rumination in sheep in the dark makes this uncertain. Dairy cows, which spend 3–4 hours less per day on the pasture than beef cattle because of the time required for milking, on average graze longer, no doubt because of the extra food requirement for milk production. The time spent by calves in grazing was found by Roy, Shillam and Palmer (1955) to be governed largely by their age, but at 5 months old in that study and at 9–15 months in another (Tribe, Gordon and Gimingham, 1952) they were grazing for as long as, or longer than many adult cattle. This may reflect the smaller intake per bite and the high nutritional requirements of rapidly growing animals.

TABLE 9.1. *Some grazing and ruminating times of cattle and sheep*

Type of animal	Grazing time (hrs) Average	Range	Ruminating time (hrs.) Average	Range	Number of 24-hr. observations	Number of animals	Reference
Dairy cows	6·7	6·2– 7·7	N.R.*		6	12	Hancock and Wallace (1947)
	8·4	6·4–10·1	6·9	5·5– 9·2	32	20	Hancock (1954*a*)
	6·8	4·4– 9·6	5·4	4·6– 5·8†	8	12	Hancock (1954*b*)
	6·5	4·3–10·5	5·6	3·7– 6·8	4	4	Castle, Foot and Halley (1950)
	7·0	5·7– 7·8	6·3	4·3– 9·2	10	4	Wardrop (1953)
	8·6	7·9– 9·5	N.R.		5	6	Seath and Miller (1946)
	9·3	7·3–11·5	N.R.		22	18	Waite, Macdonald and Holmes (1951)
	9·0	8·0–10·7	8·6	8·0– 9·8	20	8	Hardison, Fisher, Graf and Thompson (1956)
Beef cattle	7·5	7·0– 8·1	6·8‡		4	4	Johnstone-Wallace and Kennedy (1944)
	7·9	6·0– 9·4	7·8	5·9– 9·4	9	11	Hughes and Reid (1951)
Calves	10·6	9·8–11·6	N.R.		4	22	Tribe, Gordon and Gimingham (1952)
	7·9	5·6– 9·3	7·6	6·8– 8·9	6	5	Roy, Shillam and Palmer (1955)
Sheep	9·4	8·8–10·0	N.R.		12	5	Tribe (1949*a*)
	10·9	8·9–13·2	8·3	7·8–10·3	2	4	England (1954)
	8·6	6·2–10·9	N.R.		11	4	Hughes and Reid (1951)
	9·0	7·8–10·5	N.R.		11	Flock	Hughes and Reid (1951)

* N.R. Not recorded † 4 animals only ‡ 1 animal only.

In discussing the general pattern of the daily grazing behaviour, some mention should be made of the recorded figures for dung and urine production, water consumption and the distance travelled in each 24-hour period. As with all other grazing activities, the quality and density of the herbage considerably affects all these functions. Cattle, for which there are most observations, defaecate more frequently when grazing leafy swards than they do on older pasture of lower moisture content. It has been recorded that about 50 lb. dung,

with an average dry-matter content of about 11 per cent, was voided daily in 10–11 defaecations (Johnstone-Wallace and Kennedy 1944 Waite, MacDonald and Holmes 1951) On young leafy pastures containing only 14–18 per cent of dry matter, the food may pass too rapidly through the alimentary tract, producing almost liquid faeces with an abnormally high loss of nutrients, particularly of minerals (Frens 1955) Observers differ somewhat as to when most of the faeces is dropped but at least half is likely to be voided between the evening and morning milkings The number of urinations is usually less than the number of defaecations but reports are lacking for the volume released daily by grazing animals

Cattle on pasture have been seen drinking 3–4 times on average per 24 hours (Castle Foot and Halley, 1950, Waite *et al* 1951, Hancock, 1954*a*) and they drink more during hot weather and less in cold wet weather On young herbage of high moisture content the number of drinks is less than on grass of a more advanced stage of growth The volume drunk must vary considerably from cow to cow but under close folding conditions of grazing dairy cows were found to drink about 5 gallons per day in addition to the 9–12 gallons of water present in the herbage which they consumed (MacLusky, 1959) The total water intake of these cows was therefore appreciably higher than for cows from the same herd during normal indoor winter conditions, when 8–11 gallons per day were drunk from the water bowls plus 2 gallons eaten in the feed (Waite unpublished) In both experiments the higher milk-yielding cows drank more than cows with lower yields

On good-quality dense pasture sheep and cattle both travelled about 1 7–2 0 miles in each 24 hours (see for example Tribe, 1949*a* England, 1954 Hancock, 1954*b*), the actual distance depending mainly on the size of field, with about 80 per cent of the total distance being covered during daylight. The distance increased when animals were grazing in larger areas and in one set of observations increasing the area available from 0 5 acre to 2 5 acres increased the distance walked by bullocks from 1 3 miles to 2 0 miles (Hughes and Reid, 1951) Poor pasture, as would be expected, also caused the distance covered in search of food to increase Sheep in lush pasture walked 1 2 miles during 24 hours whereas on bare pasture the distance increased to 2 1 miles (England, 1954) and on the hills the figure would probably be higher

FACTORS WHICH INFLUENCE GRAZING BEHAVIOUR

CLIMATE AND WEATHER

Most of the grazing behaviour records come from countries in the temperate zones where the variation in temperature is usually insufficient to affect the total grazing time. In warm summer weather, however, there may be increased grazing at night, particularly if the animals are irritated by flies during the day. Johnstone-Wallace and Kennedy (1944) for example, reported that night grazing accounted for 40 per cent of the total grazing time of beef cattle during the summer months in New York State. In the warmer climate of Louisiana, day temperatures of 80–90° F. resulted in a complete reversal of the temperate-climate pattern of grazing, over 70 per cent of the total grazing time of 7·2 hours being done at night (Seath and Miller, 1946). Even with day temperatures in the range 72–82° F. Friesian cows in Fiji did 67 per cent of their grazing at night and the same proportion of their resting time during the day (Payne, Laing and Raivoka, 1951). This suggests that in hot climates, if special night paddocks are used, they should carry sufficient easily available forage to supply most of the nutrient needs of the animals. Bonsma and his colleagues (1953) have found that the less improved native breeds of South African cattle are more adaptable than European cattle to a hot climate and will range in search of food even during the hot period of the day, obtaining some nourishment, whilst the European cattle will not do so and consequently starve.

The recent report by Davis (1960) that cattle in high environmental temperatures considerably reduced their feed intake when the relative humidity increased may be of considerable importance in hot climates. He found that, at 90° F., an increase from 20 to 40 per cent r.h. caused the amount of food eaten to fall by 15 per cent, and that at 50 per cent r.h. they ate 20 per cent less. There was an increase of 4–5 per cent in the digestibility of the feed but this would not compensate for the greater lowering in feed intake.

Rain alone, in the amount encountered in temperate climates, is usually insufficient to affect the grazing activities of either sheep or cattle, but when it is accompanied by a driving wind, grazing and resting are both interrupted and the animals will seek shelter or stand facing downwind. If this happens during the day at a time when they would normally be grazing, there is often an increase in the amount of time spent grazing at night (Hancock, 1954a; England, 1954). Wind

alone has generally little effect on grazing behaviour, although at gale force grazing may be interrupted if shelter from the wind is available

DARKNESS

Except when the day temperatures are exceptionally high or when heavy rain and wind have delayed grazing, both sheep and cattle stop grazing as soon as it becomes dark, about one hour after sunset (Hughes and Reid 1951, Waite *et al*, 1951, Hancock, 1954*b*) When the period of darkness is short, as in May, June and July in temperate northern latitudes, there may be no further grazing until first light, but as the season advances and the nights lengthen, grazing during darkness increases up to periods of about 2 hours

THE INDIVIDUALITY OF GRAZING ANIMALS

As might be expected, the amount of time spent in grazing largely governs the weight of the dry matter eaten (Brumby, 1959) but the factors which limit the appetite of the individual grazing cow are complex In a given environment the maintenance requirements will depend on body size and these requirements will be added to in the later stages of pregnancy and foetal growth In dairy cows milk production will greatly increase the amount of food required. Although some physiological control of appetite can no doubt operate in ruminants, most consideration has been given to the physical aspects because of the bulky, fibrous nature of much of their food The amount of the indigestible residue ('ballast') from this type of feed has been suggested by Lehmann (1941) as a major factor governing appetite and he considered that for a cow weighing 1,100 lb satiation was reached when the quantity of 'ballast' in the digestive tract amounted to 9 5 lb Results obtained by Voisin (1954) agreed with this concept but this author also concluded that for animals grazing pastures of high fibre content appetite was affected by the work of chewing In addition to the limiting effect of the amount of indigestible material, Blaxter and his colleagues (1956) have drawn attention to the importance of rate of passage of the feed through the digestive tract

From considerations such as these it is clear that, although milk production in dairy cows will be a major factor governing the feed intake and hence the grazing time of dairy cows at pasture, a simple relation between the two is not necessarily to be expected Brumby (1959), in work with Jersey and Friesian cattle in New Zealand, found a positive relationship between grazing time and milk production but

other workers have not. Castle, Foot and Halley (1950) recorded one cow giving 54 lb. milk per day as grazing for 5·3 hours whereas another cow in the same group producing 36 lb. milk grazed for 6·6 hours. A month later the first cow, then giving 46 lb. milk per day grazed for 10 hours. Waite *et al.* (1951) similarly found no direct connection between grazing time and the daily, or the 180-day, milk yield of 18 cows in one herd. For six of these cows, whose grazing time had been recorded on several occasions in two successive years, the average grazing time of each cow in both years was very similar irrespective of stage of lactation and milk production and, ranked by length of grazing time, the order of the six cows was the same in both years. Hancock (1954*b*) in his observations on the grazing behaviour of twin cattle has shown that the difference in average grazing time between members of pairs of twins was very small, averaging only 7½ minutes in 6–8 hours, while the range between different pairs was as much as 138 minutes. He also found that the rumination times of the various pairs of twins was independent of their feed requirements and in a stall-feeding trial the same amount of feed caused different animals (non-twins) to ruminate for different lengths of time.

It can be seen from the values recorded for sheep in Table 9.1 that the grazing times of individual animals also vary considerably from each other even in the same environment. In addition, account must be taken of the vastly different environments experienced by lowland sheep grazing cultivated pastures and the semi-wild hill sheep grouped on their self-selected mountain hefts. Although the grazing behaviour of hill sheep formed the subject of several early studies, it is only in recent years (in the United Kingdom at least) that a comprehensive and systematic approach to this complex problem has been made (see, for example, the reports of the Hill Farming Research Organization, 1954–8, and on Hill Farm Research, 1951–3).

The large part that animal individuality plays in the observations of grazing behaviour must always therefore be kept in mind in interpreting the results of experimental work where the number of animals employed is necessarily limited.

feeding value than stem this has given rise to the theory that animals instinctively choose the type of vegetation best likely to meet their nutrient requirements This hypothesis will be discussed later, but in regard to grazing behaviour the important fact is that the fibre and lignin contents of leafy material are lower than those of the stem The rate and extent of the breakdown of forage during rumination depends to a large extent on its degree of lignification and since the lignin content of herbage increases with age, the stage of growth exerts a considerable influence on grazing and rumination times

As would be expected, therefore, stemmy herbage causes long rumination times whereas with leafy material, which is more easily broken down, ruminating times are shorter (Hancock, 1954*b*, Halley 1955) Van der Kley and van der Ploeg (1955) have demonstrated a close positive relationship between ruminating time and the weight of fibre eaten by dairy cows while grazing and the longer ruminating times necessitated when cattle graze stemmy herbage are usually accompanied by short grazing times Because of the high dry-matter content of herbage in an advanced stage of growth the animal will obtain more dry matter per grazing hour than with leafy material but much of it will be indigestible The longer time required by such material to pass through the digestive system (Balch, 1950) may also delay to some extent the desire to resume feeding

The most continuous and systematic work on the grazing behaviour of cattle has been done by Hancock in New Zealand and he has introduced the concept of the ratio of the ruminating and grazing times, rt/gt, as an indication of grazing behaviour His conclusions on the effect of pasture quality and availability are summarized in Table 9 2 It can be seen that the rt/gt value does not in itself characterize a pasture

TABLE 9 2 *The effect of the quantity and quality of herbage on grazing behaviour* (Hancock, 1950)

Quantity available per cow	Quality	Grazing time (gt)	Ruminating time (rt)	$\frac{rt}{gt}$
Abundant	high	short	short	low
Abundant	low	short	long	high
Abundant	mixed	long	long	high
Small	high	long	short	very low
Small	low	long	short	low

but if, for example, the quantity of forage available is sufficient, the ratio can give a useful indication of quality. McCullough, Sell and Neville (1954) under such conditions found a marked decrease in the weight of forage eaten and a rise in the rt/gt value as the quality of the herbage decreased. In one set of observations of dairy cattle grazing a fescue pasture, dry-matter intake per cow fell from 34 to 27 lb. per day when the dry-matter digestibility decreased from 74 to 63 per cent, causing the rt/gt ratio to rise from 0·6 to 1·3. In an experiment in which dairy cows were strip-grazed on grass at different stages of growth and were afforded little chance for selective grazing, Waite *et al.* (1951) found that they grazed for 9–10 hours on young grass containing 17–18 per cent crude protein and for steadily decreasing times on the poorer quality grass, grazing for only 7·7 hours on herbage containing 8·5 per cent crude protein. Despite this, the weight of dry matter eaten on all types of grass was approximately constant within the accuracy of the intake measurement but the amount of digestible nutrient obtained varied considerably and milk yields fell rapidly on the poorer quality grass (Holmes, Waite, Fergusson and Campbell, 1950).

Changes in the quality of herbage are frequently accompanied by changes in the quantity available and grazing behaviour is thus affected by both simultaneously. A common occurrence is the decrease in both the quality and quantity of the herbage when cattle or sheep are kept in the same field or paddock for several days. Van der Kley and van der Ploeg (1955), for instance, record that during three days' grazing by dairy cattle the digestible crude protein content of the herbage fell from 10·8 to 6·6 per cent, the starch equivalent of the dry matter from 52 to 47, whilst the fibre content rose slightly. During this time the dry matter available fell from 3,270 lb. per acre to 760 lb. per acre and grazing times increased as a result. Under somewhat similar conditions, Waite *et al.* (1951) found that whereas the average grazing time of a group of dairy cows on the first day in a new paddock of good-quality grass was 7·7 hours, it rose on the second day to 9·4 hours and on the third and fourth to 9·8 hours. Morgan (1951) has also reported that cows turned into pasture previously grazed by a large herd increased their grazing time by 12 per cent compared with their behaviour on fresh grass. Thus, as the supply of forage decreases, cows have more difficulty in satisfying their appetite and consequently graze for longer times. On the other hand, where a pasture has grown faster than the cows can eat it, the quantity available may be

high but the quality low, and as has been mentioned, this usually results in short grazing and long ruminating times and, with dairy cattle, a drop in milk yield

When the quality of a pasture is mixed, grazing time may increase as a result of the greater amount of selection required (Hancock, 1950), but where sufficient herbage is available and the animals eat both young and old grass, the grazing time may even be slightly shorter than when young herbage only is available (Tribe, Gordon and Gimingham, 1952)

The density of the sward, as distinct from the total quantity present, is also a factor influencing grazing time, since the amount obtained with each bite is greater the denser the sward On a dense first-class, permanent ryegrass pasture a group of close-folded dairy cows grazed on average over the season 1 hour less per day than when on a more open cocksfoot ley, although the weight of dry matter eaten on both pastures was very similar (Waite *et al*, 1951) The amount and density of the herbage is therefore most important in those systems of management in which cattle are allowed to graze for only a limited time on high-quality grass before being turned on to poorer pastures

THE PALATABILITY OF HERBAGE

Studies of grazing behaviour might be expected to throw some light on whether some pastures are more palatable than others Unfortunately palatability is a subjective attribute and one which is difficult to assess Even under rigorously controlled conditions, the judgement of the palatability of a foodstuff by human beings varies considerably from one individual to another The difficulty for man of determining what in a pasture is pleasing to the taste of sheep and cattle therefore needs no stressing and to equate herbage palatability with succulence only, for which much can be said, may obviously be very inadequate

Many species of animals have a liking for food which to our taste is sweet and it has been suggested from time to time that cattle like sweet foods Plice (1951), for instance, found that cattle would eat grasses and herbs which they had previously rejected if these were sprayed with molasses or a saccharin solution It is difficult to decide, however, whether an appreciation of sweetness is a factor of much importance in the selection of certain species of grasses by the grazing animal Although it is true that the concentration of the sweet-tasting sugars, glucose, fructose and sucrose, is highest in young grass (Waite and Boyd, 1953), there is rarely more than about 0 2 per cent of

glucose or fructose present in the fresh grass and usually less than 1 per cent of sucrose. Fructosan, another soluble carbohydrate, although present in larger quantities is a polysaccharide and, by our standards, is tasteless. If, therefore, sweetness plays much part in the choice of herbage, sheep and cattle must be able to distinguish between grasses in which the differences in sugar concentrations are small and all at a low level.

An interesting experiment by Bell (1959) showed that goats could clearly discriminate between various solutions representative of the four primary tastes, sweet, bitter, sour and salty. The goats studied tolerated very much higher concentrations of bitterness than did oxen and, on the other hand, did not refuse the strongest glucose solution (35 per cent) offered to them. The lowest concentration of glucose solution presented (5 per cent) was preferred to tap water and it would have been most interesting to know whether they were able to distinguish sweetness at the lower concentrations likely to be met in pasture by the grazing animal.

A further complication which affects many field trials designed primarily to establish the relative palatabilities of various herbages for sheep or cattle, is the question of herbage availability. If, as in the experiments made by Reid (1951) and Ivins (1952), the various strains of vegetation offered differ in their earliness of growth, it would be expected that in the spring animals would be found eating those plants which had made sufficient growth to be easily grazable. As the season advanced, unless some cutting technique were adopted, the early strains would then be relatively neglected in preference for the younger material. This, to a large extent, is what was observed by these authors. Similarly, if a plant such as ribgrass (*Plantago lanceolata*) by virtue of a vigorous root system can withstand repeated defoliation, it is likely to be heavily grazed and although this may be partly because it is extremely palatable, it might also be simply because it is available when less vigorous or slower growing plants are not. A true idea of animal preference could therefore only be obtained if all the species offered were available in equal quantity and at the same stage of growth at the same time, a condition rarely, if ever, met in practice.

The effect of the succulence of the herbage on animal choice can be seen in Milton's (1953) observations of sheep on undeveloped grassland in Central Wales. He recorded the degree to which the various plants or plant associations were grazed throughout the year and found that in spring and autumn the plants with green leaves were heavily

grazed in preference to those with yellow or withered leaves In summer, when all the plants were green, the sheep grazed mainly on grasses and neglected the heather and rushes they had grazed in winter and spring Very similar observations were recently reported by Cowlishaw and Alder (1960) who noted during winter grazing by sheep and cattle that it was the greener grasses that were selected first In further trials these authors also concluded that plants high in water-soluble components such as minerals and carbohydrates were attractive to the animals but whether this was a determining factor is not easy to decide The interesting observation of Hunter (1960) that hill sheep showed a marked preference for the vegetation growing on mineral soils compared with that growing on peat may also be connected with the question of nutrient availability

Thus although it is undoubtedly true that sheep and cattle, if allowed, do show preference for certain plants or parts of plants, whether this is because of the greater palatability of this vegetation or whether it is because only these particular plants are available at a suitable stage of growth for grazing, is still not clear

HERBAGE SELECTION BY THE ANIMAL IN RELATION TO ITS NUTRITIONAL REQUIREMENTS

A question of considerable practical importance is whether sheep and cattle are guided in their preference for certain types of vegetation by some nutritional instinct If this were so then observations of animal behaviour could serve to indicate the type of pasture composition best suited for these animals Because cattle have frequently been seen to spend some time grazing in the rough grass and weeds at the bottom of the hedgerows surrounding a cultivated pasture or even on the hedgerow itself, a school of thought exists (e g Stapledon, 1948) which interprets such behaviour as indicating the recognition by the animal of a lack of some constituents in the grasses and clovers provided in the pasture but which are present in the hedgerows Analysis of the weeds so consumed has shown that they are usually richer in trace elements such as copper and cobalt and often in calcium phosphorus and magnesium than young grass although the difference in the quantity of the major elements may not be great Both calcium and phosphorus are required in considerable quantity for growth and milk production and this is adduced as one of the reasons for the cows' preference for the weeds One point often overlooked however is that the amount of these elements obtained by hedgerow

grazing is small compared with what the animal normally receives from the pasture, although this criticism would not apply to trace elements present in the weeds if they were completely absent in the grasses and clovers. Thomas, Rogerson and Armstrong (1956) have shown that a pasture containing more than 20 per cent of herbs produced appreciably less dry matter per acre than herb-free pasture and the digestibility of the protein was considerably reduced. These are disadvantages to set against the increased amount of mineral elements provided which, so far, have not been clearly shown to confer equivalent benefit on the grazing animal.

The only controlled experiment attempting to investigate the effect on cattle of including herbs in pasture is that by Tribe, Gordon and Gimingham (1952). These authors compared the increases in live weight of two similar groups of Ayrshire calves from May to September when one group grazed on a weed-free pasture and the other group grazed on another part of the same pasture which contained, in addition, both natural and sown weeds. To ensure that the weed-free pasture did not produce mature 'browse' by growing more quickly than it was grazed, this sward was topped with a motor mower when necessary. There was no significant difference in health or in live-weight gain between the two groups of calves during the experiment nor at the end of the period, despite the requirement of these young, growing animals for large amounts of minerals for bone formation. This suggests that, for this class of stock at least, weeds and 'browse' were not a necessary part of the diet. As these authors recognized, a similar trial using adult cows from the calf-bearing stage to the end of lactation would be extremely interesting.

As previously mentioned, the well-known habit of grazing animals of selecting leaf rather than stem has often been taken as evidence of their nutritional wisdom since leaf contains more digestible nutrients than stem. It may be so, but certain physical considerations should also be taken into account. Sheep and cattle have front teeth only in the lower jaw and a pad of hard tissue in the upper, so that in the act of grazing, herbage is torn off the plant rather than bitten. It seems reasonable, therefore, when easily torn leaf is available that it should be eaten first in preference to the tougher stem. Moreover, as the animal puts its head down to graze, the upper leaves of the grass or clover are the parts of the plant presenting themselves first and there is no obvious reason why the animal should disregard these and search for the stem at a lower level. It is very noticeable when cattle are

close-folded that the herbage over the whole area is grazed in definite steps, the upper leaves first, followed by leaf-bearing stem and finally, if the cattle are forced to it by strict rationing, the almost leafless stem. One rarely finds cattle eating a small area down to the leafless stem whilst any more leafy herbage is still available Sheep avoid stemmy material to a greater extent than cattle and this again may be partly because of the mechanical difficulty involved in gathering it

The first need of an animal is presumably to obtain an adequate supply of energy-producing food, and by eating mainly the leafiest material the grazing animal does this It so happens that at the same time it obtains large amounts of digestible protein, often more than it requires (see, for example, van der Kley and van der Ploeg, 1955) Good pasture management therefore should aim to supply the necessary nutrients as efficiently as possible, without either wasting good-quality herbage on the one hand or decreasing animal production by providing indigestible material on the other Unfortunately, this is easier said than done and the management of pasture to provide what is best for the animal is often not the one that is best for the pasture and *vice versa*, although the practice of close-folding or rotational grazing goes some way to satisfy both demands

In an endeavour to determine whether sheep could instinctively select a suitable diet when given a free choice, Gordon and Tribe (1951) offered eight penned, pregnant Cheviot ewes three foods, one high in protein, one high in carbohydrate and a third of chopped hay, all supplemented with minerals All eight sheep chose a diet too rich in carbohydrate, with ratios of protein to starch ranging only from 1 7 to 1 12 instead of the 1 5 ratio said to be more suitable All got too fat and inactive and all ate much more food than normal, about 4 lb of dry matter per day compared with a more usual amount of 2 5 lb These ewes became so inactive in the three or four weeks before lambing that they then actually ate less than the amount required to produce and feed their lambs and only two healthy lambs were reared. One ewe died and one became ill Although these penned sheep were clearly incapable of choosing a diet suitable for their own and their lambs' well-being, this result can only apply to sheep under the particular conditions of this experiment. The results are extremely interesting and continuation of this type of work using other feeding systems is necessary

It is well known that deficiencies of both major and minor mineral elements affect animal health and production and since such deficiencies

are much less immediately apparent to the farmer than a lack of herbage bulk or quality, it is important to know whether the grazing animal can itself recognize and rectify this type of nutritional deficiency. The evidence is somewhat contradictory but this may partly arise from the experimental techniques used and the different degrees of mineral malnutrition suffered by the animals used by the different workers. Gordon, Tribe and Graham (1954), for example, offered two mineral mixtures, only one of which contained phosphorus, to hill sheep and cattle grazing on phosphorus-deficienr herbage and whose blood-phosphorus levels were only half the normal value. The experiment lasted for one year and in that time although more of the phosphate-containing mixture was eaten, the difference was not statistically significant and the more important finding was that the weight eaten of both mixtures was small compared with the animals' requirements. There may be many reasons for such a result. The grazing area, for example, was large compared with the number of places where the minerals were available. There were only eight groups of troughs for 90 cattle and 500 sheep in an area of 5,500 acres, much of it mountainous country, and trough-feeding would be something of a novelty for such sheep. Again, it is possible that the chronic deficiency of phosphorus in their blood did not create a desire for the mineral and that they failed to recognize or associate any benefit accruing from a consumption of the phosphate mixture. They may in addition, have disliked the taste of the minerals. In contrast, Stewart (1953) noted the marked preference by sheep in a cobalt-deficient area for pasture that has *been top-dressed with cobalt sulphate at the rate of 2 lb. per acre.* There was no difference between the pasture on the dressed and undressed halves of the field except in cobalt content (0·3 parts per million). Stewart's experience however, agrees with that of Tribe *et al.* (1954) in that in another cobalt-deficient area he found that sheep did not eat a cobalt-rich mineral mixture placed in troughs. Whether missing trace elements are more efficiently provided via the herbage than as mineral supplements, particularly for hill sheep unused to trough feeding, is of considerable importance.

From results such as those quoted it is obviously difficult to determine whether cattle and sheep, the former often grazing under conditions which restrict their choice of herbage, can sense and remedy minor but important nutritional deficiencies. Field experiments usually contain such a large number of variables that the results are difficult to interpret, whereas more controlled experiments may give

apparently clear-cut results which are not directly applicable to the animals in their normal environments The field experiment with relatively small numbers of animals, under as controlled conditions as possible and repeated sufficiently to eliminate or minimize 'individuality' would seem to offer most chance of progress in this interesting and important subject

THE SENSES USED IN HERBAGE SELECTION

Sight and smell are probably of equal importance in the selection of food by the grazing animal but taste and touch no doubt play a part as well It is difficult to determine experimentally the importance of the various senses and only a few attempts have been made to do so In one experiment Tribe and Gordon (1949) tried to determine whether six sheep could recognize colours by their ability to associate blue light with a palatable feed and red light with a sawdust feed Over a 70-day period none of the sheep went regularly to the palatable feed in the blue light when offered the choice and the authors concluded that the sheep were colour-blind Such an experiment leaves unresolved, of course, the question of how well sheep can remember an association once discovered nor does it allow for the natural inquisitiveness of the animal This result is, however, in accord with the view now gaining acceptance that although sheep and cattle and many other animals possess cones and rods in the retina of their eyes (Trautmann and Fiebiger, 1949) only apes, monkeys and men of the mammals possess colour vision It may be remembered (p 297) that Milton (1953) noted the preference of sheep for green leaves as opposed to yellow, brown or withered ones but even with monochromatic vision such colours, by their different light-reflecting powers, would probably be distinguishable

There seems little doubt that sheep and cows, like many other animals, possess a sense of smell and often appear to use it in herbage selection As the result of an indoor experiment with sheep, Tribe (1949*b*) confirmed this but suggested that if sheep were continually in the presence of the smell of grass and clover, as when grazing, their sensitivity to these smells might be diminished It is also possible that the sense of smell is used less to distinguish between plants than to recognize the presence of objectional material such as dung and urine

It is impossible at present to say to what extent a sense of touch is used, if at all, in herbage selection A recent histological study has shown that in the epidermis of the cow's muzzle there is a nerve structure not

unlike that present in the human gum (Nisbet, 1956). This could presumably provide a very sensitive organ for distinguishing between the feel of various plants and may be used in the often-observed rejection of hairy and spiny plants.

THE EFFECT OF FEED SUPPLEMENTS ON GRAZING BEHAVIOUR

The work described so far has dealt with animals receiving all their feed from grazing. A question of some practical importance is how the normal grazing behaviour, particularly of dairy cows, is affected when the animals are also given some supplementary feeding. The reasons for giving supplements are various; it may be in an endeavour to increase milk yields or maintain them at a high level, or it may be to eke out pasture by supplying hay or silage or, by providing starchy food in autumn, to balance the high-protein pasture obtainable under a system of controlled grazing and heavy fertilization.

Most of the work done on this subject has been with dairy cows and the results suggest that the difference in grazing behaviour of supplemented and control cows is not very great. MacLusky (1956) measured the herbage intake and the milk yield of two small groups of Ayrshire cows during four one-week periods. One group received 8 lb. of concentrates per day in addition to the feed obtained by grazing, while the other group received none. The grazing behaviour of the animals was observed for one 24-hour period in each of the four weeks. His results are summarized in Table 9.3.

TABLE 9.3. *The effect of feeding a concentrate supplement (8 lb./day/cow) on the intake, production and grazing behaviour of dairy cattle* (MacLusky, 1956)

Group	Herbage dry-matter intake (lb /day)	Milk yield (lb /day)	Grazing time (gt) (hrs)	Ruminating time (rt) (hrs)	$\frac{rt}{gt}$
Control	23·3	27·4	6·8	5·8	0·86
Supplemented	20·5*	29·8	6·0	5·4	0·90

* Difference significant at 0·2 per cent level.

Feeding concentrates resulted in a reduction in the amount of herbage dry matter obtained by grazing, equivalent to about one-third of the weight of concentrate fed, while the amount of herbage eaten per

hour by the two groups remained the same The total weight of food eaten by the supplemented group, although higher than that eaten by the control group, required less rumination than the all-grass diet. MacLusky reports that when the grass offered was of poor quality the difference in grazing time between the two groups increased, the supplemented cows reducing still further their intake of herbage This suggests that to try to improve the diet of animals feeding on poor-quality pasture by providing a concentrate supplement may, to some extent, be self-defeating since their reaction may be to eat less of the poor-quality pasture The average increase in daily milk yield of 2 4 lb per cow by no means paid for the concentrates and the additional labour involved It would be interesting to see this experiment repeated with high-yielding cows which might have more difficulty in obtaining sufficient nutrients for their maintenance and production solely by grazing Results similar to those of MacLusky were obtained by Hardison, Fisher, Graf and Thompson (1956) in America when the provision of 6 lb of grain per cow reduced grazing time by 7 5 per cent

Silage as a supplement for grazing cattle has been reported by Percival (1955) also to reduce the amount of grass eaten In his experiment the total weight of dry matter obtained from silage plus grazing was less than on grazing alone The digestibility of the organic matter of the silages provided was only 59–64 per cent, and the energy and time required to digest the supplement appeared to cut down the intake of the better-quality herbage to the detriment of animal production.

Under the hot summer conditions of Louisiana a hay supplement given to dairy cows fed also on good pasture and grain had little effect on animal behaviour or production (Seath and Miller, 1947) About 5 lb of hay was eaten, usually at a time of day when the control group was not normally grazing but the proportion of time spent in day and night grazing was the same for both groups Cows eating the largest amounts of hay grazed for about 40 minutes less than the control cows and milk production was not appreciably affected

The evidence therefore suggests that when cows are fed supplements they react by grazing for a slightly shorter time and this, no doubt, represents a saving of grazing energy and of pasture If the supplement is easily digested there will be a further saving of energy from the reduction in the amount of rumination required but the reverse will be true if the supplement is of low digestibility For dairy cows

already producing their maximum yields on good-quality pasture, supplements appear unlikely to cause any marked increase in milk production. Starchy supplements, however, which have been found in winter feeding trials to increase the solids-not-fat composition of milk, might well be used to improve milk composition in late summer when it is frequently low.

CONCLUSION

Perhaps the most striking result of the many observations of grazing animals has been to show the regularity of the life of the grazing animal in any given environment. So long as there are no extreme changes of weather and the herbage is adequate in quantity and of a reasonable quality, the pattern of grazing, ruminating and resting remains remarkably similar from day to day. Even when new systems of management are introduced, such as close-folding, the only effect is to alter slightly the time spent in the various activities and not the period of the day in which they are done. There is, of course, wide variation between individual animals in grazing habits and the little evidence available suggests that such habits are, at least in part, genetically determined.

The deleterious effect of poor-quality herbage on animal production, particularly on milk yield, is generally known although surprisingly often tolerated in practice. Observational studies have shown that both sheep and cattle take longer to ruminate such material and that the time spent in grazing it is usually short. There is evidence that the weight of herbage dry matter eaten is reduced when the fibre content is high and, since its digestibility is always lower than that of young material, the animal usually receives less nutrients than it needs to maintain production.

There is still some controversy as to whether the grazing animal can select herbage which provides the best diet for itself, and, indeed, whether modern pastures grown from simple seed mixtures allow the animal sufficient choice of material. There is little doubt that such pastures, if properly managed, provide energy and protein in a form which allows the grazing animal to obtain its needs without necessitating any real selection of herbage. Moreover, as long as a reasonable amount of clover or other legume is present in the pasture, the amounts and proportions of calcium and phosphorus will probably be adequate also, except perhaps for the high-yielding cow at the peak of lactation.

Whether such pastures provide all or enough of the necessary minor elements is not so clear, largely because the importance of many of these elements for cattle is only now receiving much attention On the little evidence available, it appears that cattle and sheep suffering from major or minor element deficiencies do not relish straight mineral mixtures containing the missing element They may, however, show a preference for herbage that is rich in the particular mineral

It is clear that, from the point of view of the agriculturalist, many of the studies of grazing behaviour are less useful than they could have been because no measurement of animal production was included. This surely points the direction for future development of this interesting subject, as a useful and probably necessary accompaniment of experimental work designed to improve grassland management and animal husbandry rather than as a subject in itself There is, for example, the outstandingly important question of why animals of apparently similar capabilities vary so widely in their ability to convert grassland and other fibrous foods to meat and milk It is not suggested that the answer to this question is likely to be provided solely by studies of grazing behaviour, since rumen metabolism, animal health and digestive efficiency are all probably more important Nevertheless, an accurate record of the animal's activities in the field, coupled with quantitative estimates of herbage intake, herbage digestibility and a record of animal production would provide results which could usefully serve as a guide to further field and laboratory experimentation

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CHAPTER TEN

Dairy Cattle

C LINE

Introduction—Farm layout, fencing and watering—Efficient herbage conversion—Methods of pasture feeding—Supplementation of herbage diets—Conservation of herbage—The balance between sward and cow

Pasture herbage is comparable with the natural food of cattle and is also the cheapest available source of nutrients which can be produced for feeding the cow To these two features, sufficient in themselves to justify the maximum use of pasture and pasture products for cattle feeding, can be added the fact that well-managed grassland is capable of outyielding, acre for acre, most other crops that can be grown for this purpose (Fowler, 1946, Holmes, 1951)

In a country where cost of land, compared with other production costs, has in general been relatively low, output per acre has not been regarded as very important by the producer, provided he is fortunate in having an adequate area for economic operation In times of national shortage the high productive potential of the pasture-fed cow has been well recognized The high-yielding cow is in fact the best converter of roughages to human food (Godden, 1948, Hodgson, 1952)

Even the most intensive production from pasture can be obtained with a modest labour requirement, the crop being particularly adaptable to mechanization The point has almost been reached where it is possible, as with corn growing, to do all operations without leaving the tractor seat The work can be done with little physical effort at fairly high speeds and with as much power as we demand Pasture is bound to replace row crops used for stock feeding which have a high labour requirement in relation to their feeding value Fully

reliance on pasture feeding are at least compensated for by the saving in other feed costs there are sound economic grounds for following such a policy Consideration of the facts suggest that these risks are very good ones Meanwhile a substantial part of our grassland research effort should be and is aimed at overcoming such problems as do arise, and so make this proposition even more attractive.

FARM LAYOUT, FENCING AND WATERING

Where it is intended that pasture production is to be fully exploited, good access to the grazing areas is an important part of dairy farm organization If the farm is predominantly concerned with dairying and the intention is to take leys in rotation over most of the farm, it is obviously desirable that the cows can be easily taken to and from any field, preferably by one man, without undue effort or disturbance on either part If outlying fields are difficult to reach they will tend to become considered as 'ungrazable' by the milking herd and will thus be subjected to the looser grazing management frequently associated with the herd followers Such fields tend to provide an undue share of conservation crops, and their swards will be inclined to lack density In contrast the easily accessible fields in the vicinity of the farm buildings will tend to be overgrazed and will often be used as exercise grounds as well, a practice which is particularly detrimental when the ground is wet Although these fields receive a large share of the farm's fertility their production is bound to suffer from excessive fouling, overgrazing and treading The practice of using fields near the dairy as night paddocks, convenient for early-morning milking, has been investigated in New Zealand (Goodall, 1951) It was estimated that 50 cows in 6 months would transfer 25 tons of dung from the day paddock to the night paddock, and with the inclusion of transfer as urine, this would be equivalent to 2 cwt of superphosphates, 3 cwt of 30 per cent potash and 5 cwt of sulphate of ammonia Where the night paddock is relatively small the effect would be accentuated. In addition about 1½ times this quantity of plant nutrients would be deposited on roads and in the cowshed After years of such translocation fertility trends develop (Sears, 1950) and the use of the modern muck spreader is often needed to correct this tendency

Ideally the farm buildings should occupy a central site, with a correct balance between the number of milking cows and the grazing acreage Herd size, mainly because of the problem of the cows travelling to

and from the grazing areas between each milking, is generally limited to units of 60–70 cows, the tendency being to split larger numbers into more or less independent herds, even when the cows are on the same farm. Regrettably, farm layouts are often inherited which were not devised for dairying on a large scale and certainly not with labour saving and mechanization in mind. Considering that these trends are sure to continue there are strong grounds for making a fresh start when opportunity presents itself, rather than perpetuating an existing jumble of buildings, perhaps on the wrong site, by additional investment.

Farm roads, if fully fenced and gated, can sometimes be arranged so that the cows can be allowed to travel back to the grazing area after milking on their own. Frequently one field has to be passed through to get to another, this fact sometimes being advanced as a sound reason for not really cropping a piece of land at all. The access field becomes a reservoir of weeds and rough grass in summer, a morass in winter, which, when it produces what little it can, only serves to impede cattle handling. By the construction of a light fence along one side—an electric fence serves very well—the cows can be confined to a narrow lane and the remainder of the field put to a really productive purpose.

There is a tendency to root out hedges and fill in ditches, converting the farm into a few large expanses devoid of fences. General management is simplified by this tidying up and large areas are much easier and quicker to deal with so far as mechanization is concerned. This tendency towards 'prairie' farming, while very suitable for pasture conservation, does not tie in well with the limitations of herd size and knowledge that extensive uncontrolled grazing does not lead to the best pasture production and utilization. The ideal conditions for grazing management are therefore rather in conflict with modern trends. An easy method of economical subdivision is needed, which can be quickly removed when not needed.

The two methods of fencing chiefly used for this purpose are light post and barbed wire or the electric fence. Barbed wire, invented intentionally to be unpleasant, is also relatively expensive, particularly if the area is only grazed, say, 4 years out of 8 in a rotation. When barbed wire is used, especially where cows are closely confined, the strands on a level with the udder should be of plain wire. Injured udders, apart from being troublesome to milk, are very liable to become infected with mastitis organisms with serious consequences for milk production and hence the value of the cow itself. The more

intensive the management the more the cows are likely to be confined in yards, parlours and reduced grazing areas. Apart from any humane aspects, it is just sound economics to remove sources of injury. Dehorning should be an essential part of the routine.

Electric fencing is far cheaper than barbed wire, easier to erect and recover and less liable to cause injury. No discussion concerning grazing and dairy cows could be complete without due consideration of the place of electric fencing. It is remarkable that a technique which was regarded at first as something of a novelty, not perhaps to be taken too seriously, has within a couple of decades become a well-recognized tool which on many farms is as much a part of the everyday life of the cowman as the milking machine. The main use of this type of fencing is for temporary purposes, due to its low cost and high speed of construction and recovery. Unfortunately it cannot be considered completely stockproof, although of course this is true to some extent of most forms of farm fencing. All aspects considered it certainly has no equal for the subdivision of fields and even its use as a boundary fence is not unknown.

Details of equipment, construction and maintenance of electric fences are dealt with in a publication devoted to this subject (Line and Burton, 1957). Consideration of their uses for grazing control are left to the chapters on grazing management, since electric fencing is only a tool for achieving a particular end. That we may need to adjust our ideas about strip-folding does not mean that there is no use for the electric fence, for even those who carry pasture to their cows in yards and self-feed silage still find applications for the electric fence in and about those yards.

A good supply of water is essential for milking cows. Lack of water on pasture even overnight, will almost certainly reduce milk yields at the following milking although the effects will depend on conditions at the time. It has also been suggested that yields will suffer if fields are large and therefore cows may have long distances to travel for water. If this is the case it is apparent that cows can restrict their intake of water voluntarily much as they reduce their intake of herbage when the sward is coarse and unpalatable. Therefore it appears sensible to encourage maximum intake of water by making access as easy as possible.

During a grazing experiment it was possible for two seasons to record the amount of water consumed daily by individual cows fed on all-pasture diets. Each cow appeared to have a characteristic requirement,

modified from day to day by pasture and weather conditions. The maximum intake of some cows reached about 18 gallons on a hot day but in cool, wet weather in spring there were some cases when certain animals drank virtually nothing at all. The average for these Friesians and Shorthorns was about 7–8 gallons a day but the average peak demand, of main interest when planning supplies, was nearly twice that amount. Ayrshires in Scotland are reported to have averaged an intake of 5·5 gallons a day (MacLusky, 1959) and appeared to adjust the dry matter of the herbage eaten to about 12 per cent. In passing, during winter it has been observed that Friesian cows fed kale of 13 per cent dry matter did not appear to need water between the morning and afternoon milkings. Feeding dry foods such as concentrates, with a dry-matter content of about 85 per cent, will naturally be expected to increase water requirements at pasture.

It has frequently been suggested that foods with rather low dry-matter content such as spring pasture, will, by virtue of their bulk, limit intake of nutrients. Grazing, as when strip-folding, is noticeably not so close on wet days but this is probably due to lowered palatability caused by increased soiling of the herbage. Even if some restriction of intake does result it would tend to occur when pasture is young and highly digestible and there is a school of thought which considers that reduction of intake at such times is desirable, as the potential of such pastures is much above that of the cow (Ivins, Dilnott and Davison, 1958). Water is normally supplied by pipe and trough although, in spite of the risks of water-borne infection, supplies from rivers and the like are often used. Very foul water is unpalatable to cows and may be largely refused, a fact which is not always noticeable. Fairly large troughs, acting as reservoirs, are an advantage where pipes are small in bore and supply pressures low, one large trough by careful siting being capable of supplying several paddocks. Polythene pipe is rapidly gaining in popularity in that it can be fairly easily installed by farm labour, although the local authority may resist such activities. When used hosepipe-fashion to extend mains this type of piping is not easily damaged on reasonably soft ground by rubber-tyred vehicles and cattle will graze round the pipe generally without disturbing it. In cold spells these surface pipes are liable to interruption by freezing, although the pipe will not burst. Water bowls on a light supporting frame are effective if pressure is good, but should be sited in a position where they are not likely to be fouled by dung, such as just beneath the electric fence. There is little point in fixing more bowls to a pipe

than it can supply at one time. Bearing in mind the amount required, carting water for cows can only be a stop-gap method considering the cost of labour.

Grazing facilities have been dealt with at some length as they need to be adequate if a good job is to be made of grassland management, particularly with regard to the milking cow, which must be moved frequently for milking and needs to be reasonably fed and watered all the time for the best results. Lack of facilities leads to poor grassland management because the amount of effort needed to do the job properly becomes excessive, particularly for a man whose daily round covers a 12-hour day. The concentrate bag offers an easy way out and it is not a great step to the point where the cow is fed mainly from this source, the pasture becoming an exercise ground between milkings.

EFFICIENT HERBAGE CONVERSION

Having made the necessary efforts to produce the most suitable herbage for the cow it seems only logical to convert as much as possible of the crop into saleable products at the earliest opportunity. The aim should be that all grazable material, which for cattle means all herbage more than one or two inches long, should be put through the animal. The longer the herbage is left on the stem the less palatable it is likely to become and hence for any particular animal the lower the daily intake for any level of appetite. Further, assuming the same degree of appetite, any herbage which is not eaten off at one grazing is even less likely to be consumed on the next occasion. The quantity of herbage which is left to decay, whether it is cut off or not, is a measure of the success or otherwise of the grazing management. It is rather a poor argument that mowings will aid in building up the fertility of the soil for they could have done that for all practical purposes just as well if they had first passed through the animal.

There is some difference of opinion as to what height the herbage should be allowed to grow to before being grazed. Before considering this aspect it is well to point out that, whatever height range is aimed at, in practice it will often be necessary to graze outside the limits set, due to wide variations in herbage growth rate compared with, in the short term, a fairly constant demand from the herd. Results from small plots, harvested by cutting, indicated that keeping the herbage short by frequent harvesting will weaken the plants and

reduce the total yield for the whole season (Stapledon, 1924). Further, the closer the plants are grazed the slower the rate of recovery (Mitchell and Coles, 1955; Brougham, 1956). This suggests that frequent very close grazing, such as might occur to a palatable patch of a continuously grazed pasture, particularly with sheep, should be avoided. Intermittent grazing by milking cattle, particularly as they are unlikely to be allowed to become very hungry, is much less likely to punish the sward to anything like the same extent. Certainly much harm can result by leaving the sward too long before grazing. Grasses become too coarse and constituents such as cocksfoot develop excessively, whilst low grazing plants, particularly clover, are suppressed. The bottom of the sward is opened up, a tendency encouraged by nitrogen, allowing more opportunity for the ingress of weeds on the resulting bare patches. Stemmy material with tussocks will result, liable to be trampled down especially if fed generously. The trampled material will rot and destroy more plants, again leaving bare patches. Recovery after such treatment, as after a late-cut hay crop, is naturally slow. While clover, under favourable conditions, will spread over uncolonized ground, cultivated grasses, unless allowed to seed, which is not in the best interests of herbage production, do not as a rule do this to any useful extent.

Rapid production, when conditions are favourable, is a great attribute of the grass crop but there is no practical economic way so far of arresting such growth when the ideal stage of development is reached although it is possible that some satisfactory hormonal treatment may ultimately be devised for this purpose. The natural tendency is to wait until the ideal stage of growth is reached before starting to graze or conserve the herbage. As utilization is bound to take some time to complete, on a large field supplying perhaps several weeks' grazing at a time, there is a strong likelihood for a considerable proportion of the crop to be dealt with well past its optimum stage of development, especially in spring and early summer when growth is so rapid. Generally speaking, the aim should be to commence conversion on the early side, with the utilization of the crop planned well in advance, rather than taking action to rectify a deteriorating situation half-way through the grazing. Herbage will then tend, on average, to be more palatable, more digestible and therefore require less supplementation. Taking a rather mature hay crop from an area intended for grazing is almost certain to upset the continuity of even the most flexible grazing plan for the rest of the season.

There are some who prefer to graze a fairly long sward on the grounds that a greater bulk is produced of a quality more suitably matched to the nutritive requirements of the cow As the average herd usually contains animals having a fairly wide range of nutritive requirements concentrate supplementation seems to be indicated under these conditions for the higher-yielding cows Some research with grazing cattle to compare the relative values of swards kept long and short is already in progress The probability is that, for cows at least a middle course, avoiding extremes in either direction is in fact a reasonable compromise for both cow and pasture The flail harvester does now offer a solution for the disposal of trodden-down long herbage but this does not make good the waste which has occurred A good reason for leaving an area of pasture ungrazed is to provide a continuity of feed supply when herbage growth has been curtailed by drought or the onset of autumn This 'storage on the stem' is not particularly good for either pasture or animal but it is sometimes an unavoidable necessity Repeated close grazing in drought tends to aggravate the shortage by delaying recovery when rain does come In autumn growth is slow and there is plenty of time to tidy up such material provided that land is not so wet that the plants and soil texture are damaged by treading thereby reducing yields the following season While winter forage alone might be suitable for store cattle (Hughes, 1954) it must be remembered that so far as milk production is concerned the nutrient content and palatability are not very high

The greater the degree of utilization of a pasture the smaller the margin of allowable error in the judgement of the minimum amount of herbage required. It is understandable that very intensive utilization might well be considered too much of a risk in the case of high-yielding cows, as a fair amount of attention to detail is required in day-to-day grazing management It is possible to organize a more foolproof system which will achieve similar or possibly even better ends. This can be done by allowing first access to the pasture for the more responsive stock and final clearance of the herbage by the other stock. For example, the milking herd could be split into a group of high and a group of low yielders Although not entailing a great amount of extra organization if this procedure is considered too much trouble an alternative is to use the herd followers or even other classes of stock to do the 'clearing up'

Two experiments each using two groups of milking cows of equal potential were carried out allowing one group to graze just after the

other as described (Blaser *et al.*, 1959). Although rationing was considered generous the milk yields of the group having first choice were superior. The group grazing afterwards must be close on the heels of the first animals if grazing of recent recovery growth, generally accepted as very detrimental to future herbage production, is to be avoided. In New Zealand the calves, pasture fed, are sometimes given priority over the milking herd in a similar fashion, in order that they should have a superior choice of herbage as well as avoiding heavy infestation with internal parasites. The extra effort entailed in operating this and other integrated grazing systems will depend considerably on the farm layout and fencing and it was for this reason that this aspect was stressed here when first considering pasture utilization. As mentioned (Ivins *et al.*, 1958) there are those who consider that pasture potential can be high above that of even the high-yielding cow and therefore intake can be restricted without loss of yield. Whether or not this is the case for high-yielding cows there are good grounds for thinking that it is true for the lower yielders and the intake of the followers could certainly be cut down when pasture is abundant. There is little reason for stunting the higher yielders until a restrictive policy has been imposed on the rest of the stock on the farm.

Grassland recording systems, which have been in existence in various forms for some time, have had considerable attention over the last few years and have claimed a number of enthusiasts. A sub-committee appointed by the British Grassland Society published a report on the feasibility of measuring production under commercial farming conditions (Barker *et al.*, 1955). A method is given of estimating the starch equivalent output of pasture to allow comparison between grassland of different types and different management systems. As admitted in the report, there are unavoidable errors inherent in the recommended procedures but these are not normally held to be so large as to vitiate application of the method. Strong criticism has been made of the method whereby full deduction is made for all concentrate foods fed, as this assumes that invariably full response to concentrate feeding will be obtained (Cooper, 1954, 1955). Considering the frequent necessity to introduce personal judgement into the estimates, small differences indicated by such a system should be viewed with much caution.

The value of the method probably lies in the fact that there are such great differences in output of good and poor grassland that these errors are perhaps relatively unimportant. Unfortunately the really bad

grassland manager is rather unlikely to be bothered with what he may well consider to be a fairly detailed system of this type. A much simpler one embodying perhaps just recording cattle grazing days and an estimate of conservation crops for each field, might serve an equally effective purpose in this case

METHODS OF PASTURE FEEDING

The simplest way of feeding a herd on pasture is to let the cows roam at will over the whole grazing area A minimum of labour, fencing and watering is required and, provided the stocking rate is suitably adjusted to this tempo of utilization, the cows will look after themselves tolerably well. They will overfeed when herbage is plentiful neglecting less palatable plants and portions of plants, only to consume this poorer material later in the season when it is even more unattractive Should severe shortage occur, due to drought for example, the only course is to feed some other food or dispose of some of the cattle Such a system is open to market fluctuations the prices of hay and cattle responding rapidly to supply and demand at such times Production per acre is unlikely to be very satisfactory but these methods are usually linked with the use of permanent pasture which is much less liable to get out of hand than a vigorous well-fertilized ley Indeed it would not be advisable to invest very much in leys and fertilizers if the resultant pasture were not to be used more efficiently for the profitability might well be reduced by such practices

A higher utilization rate in the short term can be achieved by grazing the area with more cattle than the pastures can be expected to support for a good deal of the season, making up the deficit by the use of concentrate foods If the supplementary food is rationed intelligently the output from the pasture will be improved since the output of a pasture is very sensitive to stocking rate It is common practice to regard the pasture as only capable of supplying a maintenance ration for the cow over a good deal of the season but providing this approach is profitable, economically there is no objection to it

Continuous grazing allows the cow to neglect the distant parts of the field and to utilize repeatedly and tread the areas closer to the gate Thus, in fields large in relation to the size of herd it is possible for loss of herbage production to occur from both over- and undergrazing at the same time and an uneven spread of fertility can result as well. Control of herbage growth and flowering is reduced since no area in

particular is completely utilized. For example, if half the area of a field is grazed the remainder can, if not required for grazing, be cut for conservation, but if 50 per cent of the herbage over the whole field is eaten it is more difficult to deal with the remaining trodden herbage mechanically and the end product will be soiled and of inferior feeding quality.

A superior alternative to extensive grazing is to divide the pasture into paddocks of such a size that the herbage is utilized to a desired extent in a shorter time. While recognizing that a certain amount of herbage production is bound to be lost in the course of utilization by grazing (Edmond, 1958; Blaser *et al.*, 1959) this effect is kept to a minimum by limiting the duration of utilization. While pasture plans can stand a lot of maltreatment there is little sense in abusing this attribute.

Terminology of the various ways of grazing subdivided pasture is not particularly specific. There is no fundamental distinction between rotational grazing and strip-folding, which is in turn sometimes described quite aptly as ration-grazing. These methods are best described with respect to the frequency with which access to fresh pasture areas is allowed. Ration-grazing generally implies feeding off the area allowed in a day or less, although a ration may be given to last for several days. Rotational grazing generally refers to periods longer than this, perhaps up to a week or ten days. Originally movement from paddock to paddock was implied, whereas folding suggests the temporary fencing off of a portion of a field. Obviously it is possible for the two methods to coincide in effect, although for the purposes of discussion the above definitions of time are implied.

Strip-folding indicates the forward movement of a fence, generally electric, across a field, allowing the cows a fresh strip of pasture at each move. Ideally, if the strip can be made long enough the whole of the herbage can be grazed from underneath the electric fence, the cows being unable to trample on the ungrazed herbage or to foul it with dung. The difficulty is that the size of the herd in relation to the length of the field is such that the fence generally needs to be moved several times a day to allow access to an adequate ration. Cows cannot reach under an electric fence of reasonable height for more than a yard at the most and for an average crop of 50–60 cow-days per acre capacity, some 80–100 square yards of pasture are needed daily for each cow.

Many comparisons have been made experimentally between strip-folding, usually on a daily basis, and rotational grazing. In the earlier work efforts were generally made to keep the groups of cattle equally

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A superior alternative to extensive grazing is to divide the pasture into paddocks of such a size that the herbage is utilized to a desired extent in a shorter time. While recognizing that a certain amount of berbage production is bound to be lost in the course of utilization by grazing (Edmond, 1958; Blaser *et al.*, 1959) this effect is kept to a minimum by limiting the duration of utilization. While pasture plans can tand a lot of maltreatment there is little sense in abusing this attribute.

Terminology of the various ways of grazing subdivided pasture is not particularly specific. There is no fundamental distinction between rotational grazing and strip-folding, which is in turn sometimes described quite aptly as ration-grazing. These methods are best described with respect to the frequency with which access to fresh pasture areas is allowed. Ration-grazing generally implies feeding off the area allowed in a day or less, although a ration may be given to last fot several days. Rotational grazing generally refers to periods longer than this, perhaps up to a week or ten days. Originally movement from paddock to paddock was implied, whereas folding suggests the temporary fencing off of a portion of a field. Obviously it is possible for the two methods to coincide in effect, although for the purposes of discussion the above definitions of time are implied.

Strip-folding indicates the forward movement of a fence, generally electric, across a field, allowing the cows a fresh strip of pasture at each move. Ideally, if the strip can be made long enough the whole of the herbage can be grazed from underneath the electric fence, the cows being unable to trample on the ungrazed herbage or to foul it with dung. The difficulty is that the size of the herd in relation to the length of the field is such that the fence generally needs to be moved several times a day to allow access to an adequate ration. Cows cannot reach under an electric fence of reasonable height for more than a yard at the most and for an average crop of 50–60 cow-days per acre capacity, some 80–100 square yards of pasture are needed daily for each cow.

Many comparisons have been made experimentally between strip-folding, usually on a daily basis, and rotational grazing. In the earlier work efforts were generally made to keep the groups of cattle equally

contented on both treatments and under these conditions it was found possible to do this on a smaller area of pasture when strip-folding. The cows utilized a greater percentage of the herbage present and advantages ranging from 15 to 40 per cent improvement in production have been claimed, values of 20–25 per cent being frequently quoted (Hosking and Line, 1956). Further investigations have shown that stocking rate has a very marked effect on output per acre. The higher the stocking rate the greater the degree of utilization of the herbage and the more the intake of the individual is restricted. If overfeeding normally occurs then increasing stocking rate decreases this possibility and yields will not be reduced in direct proportion to the lowered intake, hence part of the reason for an increased output per acre. It now seems probable from experiments comparing strip-folding and rotational grazing at the same stocking rate, that much or even all the differences originally found could be accounted for by differences in stocking rate (McMeekan, 1956, Campling MacLusky and Holmes, 1958, Freer, 1958, Line, 1960). The advantages of strip-folding were originally attributed to reduced waste of herbage due to treading and fouling from freshly dropped dung. Observation suggests that the amount of waste due to dung falling on to the herbage at the time of grazing is quite small. Dung contamination from previous grazings causing the regrowth of herbage to be unpalatable is the real problem and strip-folding will have no beneficial effect in this respect. So far as trampling is concerned this only becomes serious when the herbage is long for utilization by grazing. There is a natural tendency for cattle to walk to and fro behind the fold wire, subsequently refusing to eat the line of trampled herbage. This effect is particularly apparent in wet weather, so that it is easy after grazing to see the positions occupied by the fold wire each day. In wet weather, concentration of treading is undesirable and it is then better to encourage the cows to spread out over the pasture.

Strip-folding across a large field tends to be slow and in periods of rapid growth recovery behind the cows on the grazed areas occurs before the first grazing over the sward is completed. The recovering pasture may attract the cows in as little as 10–14 days after grazing and regrazing at this time is particularly detrimental to the plants. To do the work thoroughly it is therefore desirable that a second or back fence be erected behind the cows to stop grazing of the recovering plants (Line and Burton 1957). Allowing access to gates and water adds to the complications and it is not surprising if back-fencing is

neglected in practice, thereby defeating the object of the strip-folding method to some extent.

Much less effort is entailed in carrying out a rotational system. Suitably sized paddocks can be set up at the beginning of the grazing season and the need for daily adjustment of the fences, irrespective of weather, is eliminated. The more expensive easily-moved type of electric fencing is not required. If paddocks are arranged as a series of long strips, tractor work is not seriously impeded and, because the fence stays in one position, there is not so much chance of mislaid equipment becoming mixed up with machines. As rotational paddock grazing entails less effort it is more likely to attract support from those who do not feel that strip-folding is worth while.

Strip-folding ensures that the degree of hunger of the cow is kept fairly constant; at least as constant as the rationing. Cows need not be particularly under- or overfed and are therefore uniformly contented and tractable. To stock at the same rate but giving a fresh allocation of pasture, say once or twice a week, means that the cows will eat more than they require on the first few days, becoming progressively less satisfied with time. If utilization is at a high level then the cows will be really hungry on the last day or two on the paddock. This variation in food supply will be reflected by variations of the daily milk yield. Fluctuations of up to half a gallon a cow per day may result (Balch and Line, 1957; Line, 1960) but it seems that, providing the process is not carried too far, the yield per cow and therefore, using similar stocking rates, yields per acre, will be similar. More needs to be known about the effect of feed variations on lactation response before final conclusions are reached but it does seem probable that the cow has rather more resilience than was first suspected and reports of her considerable ability for adjustment to varying conditions have already been made (Hodgson, 1933; Waite, Macdonald and Holmes, 1951; Hancock and McMeekan, 1954). The effects of short periods of under-nutrition after calving on the establishment of lactation have been studied (Flux and Patchell, 1957). Five days' underfeeding had little or no effect and the effect of ten days of such treatment did not have dramatic repercussions. When this aspect is thoroughly investigated it should be possible to some extent to equate the likely loss of milk production per lactation with waste of uneaten herbage due to undergrazing and the reduced seasonal herbage production likely due to overgrazing.

One method of feeding cows on pasture herbage remains to be

considered 'Green soiling', the method whereby herbage is cut and carried to the cow kept in a yard, has been known for centuries as a means of obtaining very high yields per acre This method has come to the fore in latter years under the name of 'zero grazing' (Kennedy, Reid and Anderson, 1959), a term which does not seem particularly apt, and in any case a further name for the method was not needed As the enthusiasts are keen to point out, there are a number of advantages to be obtained from 'green soiling'. It is as well to remember there are also some disadvantages Fields that are never grazed do not need to be fenced or folded, or to have water supplies, and they can be inaccessible to cattle, by virtue of distance and obstructions such as main roads The effect of the animal on the pasture is replaced by the machine 'Grazing' time is short, hooves are replaced by tyres, dung fouling is eliminated and harrowing of dung patches and topping-over are avoided Integration with conservation is good, for equipment can be matched to the entire herbage crop and, at first sight, feeding the cows simply entails the diversion of a few loads into the yards rather than the silo In fact this is a little too easy, for a crop suitable for conversion into medium-quality hay or silage is not likely to be suitable for producing high milk yields without supplementation Difficulties have arisen because the material was not palatable enough to encourage sufficient intake Concentrates, fed to make good the deficit of nutrients, served to reduce the interest of the cows still further

Until recently this method has not been much used on the grounds that the advantages do not offset the greatly increased labour and machinery costs For every day of the 'grazing' season, feeding each cow entails bringing about 1 5 cwt of herbage into the yard and the resultant dung, urine and any refuse herbage has to be taken out again Some sort of bedding or slatted floor is also needed Renewed interest has been shown recently, probably because of advances in herbage harvesting machines and the growth in the use of the more efficient diesel tractor, but few have really got down to the equally important problem of manure disposal Suitable pumping gear does exist but this increases equipment costs still further It seems unlikely that the small farm will be able to afford such large investment in equipment, although on the medium-sized unit additional use of silage-making equipment would be an advantage Whatever harvesting machines are used they must be reliable, for failure for a day or so will seriously disturb the routine of the cows Cut grass in heaps ferments rapidly

and so needs to be harvested as required. Conversion of all crops to silage before feeding is one answer but of course losses of nutrients from silage-making are unavoidably introduced no matter how well the silage is made.

Applied correctly 'green soiling' could be satisfactory but the question arises as to whether or not the stage has yet been reached to justify economically adequate mechanization of the job. In the process of converting pasture to milk a herd of cows do a fair amount of work for us without much fuss and with few breakdowns.

SUPPLEMENTATION OF HERBAGE DIETS

Concentrate foods before the last war were low in cost and, inexpensive or not, it was traditional to place heavy reliance on their use for milk production. Generally speaking, this was and still is the easiest way of feeding the cow and such a procedure avoids worrying about grassland productivity. The feeding-stuffs merchant shoulders the worries of compounding suitable rations and competition between rival firms ensures that a reasonable job is done.

During the war, with concentrate feeding-stuffs in very short supply, it became essential to put more reliance on pasture and other forage crops. As a result there was a great dissemination of available knowledge on grassland management and the idea of treating pasture as a crop must certainly have made a great deal of valuable progress at this time. The present-day increased cost of supplementary feeding-stuffs relative to other prices has to some extent encouraged continued economy in their use. However, the general impression is that by now many have returned to the traditional system, demanding in the process that milk prices should be geared to the cost of purchased feeding-stuffs. At the other extreme there have emerged the 'forage farmers' who, during the grazing period appear to be as capable as their New Zealand counterparts in producing milk with little or even none of these commodities (Paterson, 1956). On most farms there is some choice in the method of feeding although there are in existence a number of small dairy farms unable to produce sufficient home-grown foods to carry a herd adequate to provide a living. Should it become unprofitable to feed 'concentrates' to any extent these farms would have to resort to reorganization or more diversification.

Mineral supplements may be needed, particularly for high-yielding

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Mineral supplements may be needed, particularly for high-yielding

cows, but their use in any but moderate quantities should be limited to occasions when there is known to be a definite deficiency Simply because a cow exhibits an apparent liking for minerals is rather a doubtful argument for their use The assumption is that the cow instinctively knows what is good for it, which is difficult to prove although it may be justified occasionally Generally, when mineral mixtures are offered, surprisingly large quantities are consumed initially but this intake soon declines to quite small proportions, indicating a certain novelty value perhaps, unless it is accepted that the cows not eating the supplement are those who do not need it If a cereal mixture is fed at pasture it appears to be a far better proposition to include the minerals with this, thereby ensuring that all individuals get a share and the higher yielders, normally being fed more concentrates, will receive extra minerals to compensate for heavier losses in the milk.

It is as well to appreciate that many general-purpose mineral mixtures contain quite large proportions of common salt, calcium and phosphate and these will not of course offer much protection where requirements for some other mineral are large In conclusion it can be definitely stated that milking cows have been fed on moderately fertilized pasture alone throughout the grazing season without any apparent ill effects Under pasture conditions the mineral most likely to be required, mainly in the first month of the season, is magnesium, to ward off the possible onset of hypomagnesaemia

All major dietary changes tend to upset the performance of livestock and as a general principle such changes, when unavoidable, should therefore be brought about as gradually as possible, giving some time for adjustment to the new conditions Changing cows from perhaps a hay, silage and concentrate diet to spring pasture, possibly with little or no 'concentrates', is a fairly severe alteration in feeding regime and it is advisable to take a week or so to complete such a change in order to spread the stress so caused Feeding supplements at young pasture might be beneficial in that the change-over to a pasture diet is not so drastic and the total amount of the herbage intake is reduced. Rapid changes to very lush pasture in spring are considered to be responsible for a decline in milk-fat percentage (Provan, 1952), but this does not mean that fats are necessarily always low as a result of this treatment. Neither is it certain that a lack of fibre is entirely the cause of this phenomenon. The solids-not-fat fraction very often rises when pasture feeding is introduced, suggesting that the amount of energy obtained

from the herbage is greater than that obtained from the winter rations, even when these are reasonably adequate as judged by feeding standards. In addition to this rise in solids-not-fat it is normal to obtain a substantial boost in milk yields on commencing grazing. For example, 38 cows introduced rapidly to an all-pasture diet in early spring increased in yield on average by about a third of a gallon a head per day, the higher yielders showing the greater response (Balch and Line, 1957). The change to pasture on a large commercial farm indicated a similar response (Paterson, 1956).

Scouring is often considered a disadvantage of feeding spring pasture, although it is liable to continue for quite a long period providing a supply of young herbage of low fibre content is maintained. There does not seem to be any real evidence that much harm does result. Possibly there is confusion with infective scouring and scouring resulting from digestive disturbances, which occur from time to time on most feeds. The production responses obtained at the time of turning out to spring pasture certainly suggest that any adverse effects that do occur are more than outweigbed by the advantages gained. Live weights do fall very rapidly at this time of the year, but this has been shown to be almost entirely due to a change in the weight of gut contents (Balch and Line, 1957) and accounts for the subsequent rapid rise in live weight immediately afterwards as the pasture becomes more fibrous and gut contents increase again. Once the change to pasture is completed, even when no other food is fed, it is quite normal for the live weight of milking cows to increase, at least until mid-season. In addition the condition of the coat of the cow is never better than at this time of the year, suggesting good health and generous feeding.

Fibrous foods are sometimes fed with young herbage, with the object of ensuring that butter-fat percentage is maintained and also with the intention of slowing down the rate of passage of the herbage through the tract and reducing scouring. While it has been shown that on fibre-deficient non-pasture diets a circumstance can arise where milk-fat content does definitely decline, the condition is not attributed simply to lack of fibre as measured chemically. The physical state of the fibre was considered important and the influence of the particular foods used on these experiments was not ruled out (Balch, Balch, Bartlett and Rowlands, 1953). Theoretically if food passes rapidly through the tract there is insufficient time for extraction of as large a proportion of the nutrients as might otherwise be possible.

Should the feeding of supplementary fibre be thought worth while, then palatable straw or fibrous hay will provide a suitable source more economically than by the other means, such as high-fibre cubes Providing the effect of feeding low-quality roughages is not to reduce the capacity of the cow below reasonably full productive requirements no harm will result and a certain amount of pasture may be saved early in the season when it is scarce and therefore particularly valuable In Scotland, cows were allowed access to clean oat straw (Campling, MacLusky and Holmes, 1958) The most that was eaten, on average for the season, was 0 6 lb per cow per day where a heavily fertilized sward was fed Intakes which varied considerably, were much less on a clover sward, and little straw was consumed at all in July and August It seems unlikely that such small amounts, perhaps a pound per head a day in spring could have much worth-while effect

As the season advances the pasture will tend to become less palatable and the intake of herbage dry matter will fall particularly if attempts are made to keep the degree of utilization fairly high, a desirable feature if high yields per acre are aimed at At the same time the fibre content of the herbage will tend to rise and digestibility will be declining particularly at the time of flowering It is obvious therefore that an improvement on the results obtained in the early part of the season cannot be expected In addition to a possible acceleration in lactation decline, a reduction in the solids-not-fat fraction sometimes occurs in mid-season again indicating failure to supply adequate nutrition (Riddet, Campbell McDowell and Cox, 1941, Rowlands, 1946) If pasture potential is at first above that of the cow then this is a distinct advantage, in that there is a better chance that it will still be adequate later in the season The time at which the majority of cows calve is important in this connection The price structure for milk is adjusted to encourage adequate supplies during the non-grazing period and this entails an autumn and winter calving policy, rather than 'calving with the grass' as in New Zealand (Ward, 1942) As a result quite a large proportion of the herd will be a quarter to half way through their lactation as pasture becomes available Thus, by the time the pasture starts to fall off in quality in June the cows will also be well advanced in lactation and a natural decline is to be expected irrespective of food quality Quite correctly, any downward trend in the milk production of the herd is viewed with concern and the natural reaction is to attempt to improve the level of feeding Before doing this it is well to consider

carefully just how such a policy will be economically justifiable in terms of milk-yield response compared with the cost of the concentrates required.

In spring and early summer, while the cow can obtain a good feed of highly palatable herbage, there seems to be no need either theoretically or practically for supplementation with protein foods and not a great deal of need for the use of energy foods either. The ability for good rotationally-grazed pasture herbage alone to provide for the maintenance of a 10-cwt. cow and the production of up to 5 gallons of milk per day on an intake of 30 lb. of herbage dry matter has long been recognized (Woodman, 1952). Yields above 5 gallons can be obtained and this is to be expected. For example, adult Friesian cows can average 11·75 cwt. live weight allowing a theoretical intake of 35·25 lb. dry matter, which provides 23·5 lb. of starch equivalent, assuming an S.E. of two-thirds. While a lower intake may occur in early spring when pasture is sparse, the digestibility of the herbage will be very high, perhaps 80 per cent, at this time. Such an intake should provide for a milk yield of 6 gallons per day, and in an autumn and winter calving herd there will not normally be any animals who cannot obtain their needs from good pasture in spring and early summer. This simple calculation, also supported by research at the Hannah Dairy Research Institute (Holmes, 1951), demonstrates that with *ad lib.* feeding of good pasture it is possible for the herd on average to be consuming perhaps nearly double its production requirements. This assumes that appetite will not be adjusted to milk yield, which is not actually correct but clearly the opportunity for luxury consumption exists. There is certainly a substantial safety factor, particularly for the lower-yielding cows and it is therefore surprising to find in practice that, although many produce intensive grazing pastures, these are only valued as extensive grazing or even less (Woodman, 1952).

Most experimental work has shown only small increases in milk yield which could be attributed to the supplements fed at pasture (Cooper, 1955) confirming the deductions just made. Mainly palatable foods such as sugar-beet pulp have had to be used to encourage the cows to eat them. Generally it is thought that the effect of feeding these foods is to decrease the intake of herbage but to increase slightly the total intake of nutrients. Probably as a result of this, milk yields have also been increased slightly but in the majority of cases this increase was very far from being economically worth while. In one experiment (Corbett and Boyne, 1958) 59 lb. of dry beet pulp was

needed to produce an extra gallon of milk in spring and 34 lb was required in the autumn Naturally the quality of the pasture supplemented would have a marked effect on the results obtained, but generally speaking on experimental work the pasture would be expected to be reasonably good and so would tend to minimize response to the supplements If large responses are obtained in practice the conclusion should be that something needs to be done about the pasture management rather than that pasture in general is incapable of supplying adequate nutrients

There has been much interest technically in supplementation of pasture in attempts to balance and so make use of the excess nitrogen normally present Proteins are relatively expensive to obtain in the form of supplementary food and it is logical to attempt to make the most of the generous supplies in herbage Protein feeding-stuffs were in short supply during the war and we have therefore become very protein-conscious Winter rations containing medium quality hay, straw and roots are likely to be short of protein, again focusing interest on this fraction So far it does not seem to be an economic proposition to balance excess pasture protein the energy rich foods being relatively too costly It is now considered that one of the factors limiting protein utilization in a cow's ration is a lack of sufficient energy to keep the microbial flora of the rumen active (Rook, 1959) This flora can only convert the food protein into a form suitable for digestion if it has sufficient readily available energy to do so It seems that in many ways we might do better to be more concerned with the energy value of our grazing pastures merely avoiding where possible tendencies to increase unduly the nitrogen content of the herbage by practices such as the late top-dressing of grassland with large quantities of nitrogenous fertilizers, which might even prove harmful to the cow (Hood, 1956)

Considerable emphasis has been given to the question of pasture supplementation It is quite apparent that in practice it is normal to feed large amounts of concentrate foods with even the best pasture An M M B survey of about 1,000 herds for 3 years during the month of May, when pasture is at its best showed that at this time only between 5 and 10 per cent of herds were receiving grass alone (Anon , 1958-9) The remainder were fed an average of 1 5 lb of concentrate foods for every gallon of milk produced and some roughages were fed in addition. The breakdown of these results into type of concentrate fed indicates that about 40 per cent fed a balanced cake alone and to

this could be added about another 10 per cent who fed a mixture of balanced cake and some other concentrate. Considering the time of the season in which this survey was made it is certainly time that feeding methods are reconsidered. While technically small improvements in yield can be made, the true criterion in practical farming is whether supplements are economic. Nutrients from grazing are relatively so cheap compared with other foods that fairly large improvements are required to make supplementation worth while.

CONSERVATION OF HERBAGE

While no attempt will be made to deal with the subject of herbage conservation in detail, it is worth while to consider the integration of grazing and the making of hay and silage, since these two aspects of grassland management should be made interdependent. Pasture production follows a pattern which is largely dependent on the growth cycle of the plant (Anon., 1958). Stage of plant development is in turn linked to day length but the actual bulk of the crop is controlled, very considerably on some occasions, by climatic conditions. The nutrient demands of the milking herd do not vary much from month to month, the normal aim in this country being to produce a continuous flow of milk throughout the season. Changes in herd size are after all generally brought about quite gradually, due to the cost of the stock. Ideally then, in the short term it is desirable to attempt to obtain a more uniform supply of feed rather than entertain the ideal of adjusting the numbers of milking cows to the amount of pasture available. A lot of effort has been and still is being put into achieving the ideal of producing a nutritious sward in adequate quantities for grazing all the year round (Stapledon, 1947). Although valuable advances have been made it seems unlikely that this end will be completely achieved in our climate for a long time to come, particularly so far as a ration of adequate quality for milk production is concerned.

To even out the supply of nutrients the surplus above the herd's needs must be cut for conservation. Conservation should be planned with just as much thought for ensuring future supplies of grazing as for the making of the product itself. All too often the object seems to be the storage of as much bulk as possible with only moderate concern for the feeding value of the end product. Such procedure ensures that after one heavy summer crop recovery growth will be slow, perhaps negligible, until autumn. No doubt this reduces management

worries on outlying fields but it is most unsuitable if regular supplies of grazing herbage are hoped for It is a much more flexible arrangement if a lighter first cut is conserved and the second cut can be kept for grazing if need arises

Weather conditions have tremendous repercussions on conservation programmes If our weather could be relied upon to give an adequate and foreseeable period of haymaking weather it is doubtful if so much time and effort would be spent on making silage, involving as it does the transporting of such vast amounts of water about the farm Again it is unfortunate that silage-making takes place before haymaking, since, as a safeguard against bad weather, there is a tendency to conserve a substantial part of the crop by the more laborious process Although it is folly to attempt to make good silage in pouring rain the fact remains that a satisfactory result can be obtained in the short dry spells which do occur in spring when large scale haymaking is not likely to be very practicable

It is often possible to commence haymaking early, thereby considerably lengthening the total time in which the work can be carried out The earlier the cut the better the digestibility and the quicker the crop can be dried out because of its reduced bulk If the final product is too bulky for its nutrient content it will not have a great deal of value for milk production in any case Early rather than late conservation in spring will also allow rapid recovery of the pasture and the regrowth will be more suitable for summer grazing purposes A light cut will have rather less adverse effect on grass growth than a light grazing (Edmond 1958)

Fortunately, well-conserved good-quality pasture, with a strong emphasis on the quality of the herbage crop as cut for conservation, as well as on efficient conservation itself, forms a good although more costly substitute for grazed pasture Some nutrient loss is certain to occur during conservation and so the end product is unlikely to show an improvement in feeding quality over that of the original herbage Well-conserved herbage can still satisfy a considerable proportion of the nutritional requirements of the milking cow Reference to the starch equivalent figures mentioned (Clark and Bessell, 1954, Hamilton 1957) show that the cost of grassland nutrients is considerably increased as a result of conservation and emphasizes the desirability of maximizing utilization by direct grazing All the same even the highest-quality silage and hay are still much more economical than the equivalent quantities of concentrate foods

THE BALANCE BETWEEN SWARD AND COW

Once the general principles of establishing a ley are appreciated and providing the weather is reasonably kind during the initial phases, it is not unduly difficult to create a good pasture under quite a wide range of conditions.

Making the best use of the resultant herbage is perhaps not so straightforward, possibly because it is a more long-term process. In some cases preconceived ideas concerning the feeding value of pasture and the degree to which it can be grazed without detriment to animal production are difficult to overcome. A journey through most of our farming districts generally provides ample evidence that a good deal of the herbage produced is not efficiently utilized and in some cases a considerable amount of the fodder is obviously wasted. This observation by no means applies only to the poorer grassland for often it is equally evident where a good deal of care has been taken to produce a first-class ley and the crop has been bulked up by the liberal use of fertilizers. The Milk Marketing Board survey mentioned in the section on supplementation (Anon., 1958–9) makes evident the fact that many farmers rely on concentrate foods for milk production when they have already made good provision for this requirement in the form of pasture investment.

The problem is largely one of striking the right balance between the sward and the cow. These two factors, intimately linked as they are, should be as complementary as possible but there are occasions when a certain amount of sacrifice of one or the other must be made. There is a natural tendency to attempt to maximize the monthly milk cheque without sufficient regard to the economics of doing this in terms of increased output of milk against the expense of additional supplementary foods and the rather more obscure costs of depressing the pasture productivity of the farm. Economists suggest that, for maximum profitability, the farm should be stocked as heavily as possible rather than to the lowest likely level of forage output. Taking into consideration the wide variations in herbage yields which are liable to occur owing to climate and management, this means that, on occasion, supplies of herbage are bound to fall short of requirements. The manager is then faced with the problems of underfeeding, overgrazing and the expense of supplementary foods. The success he achieves in avoiding such circumstances in the first place and the skill with which he compromises these situations when they do arise, largely

determines his efficiency in grassland management Unfortunately in the case of perennial crops mismanagement at one period of the year may not only reduce yields at the time but generally has a marked influence on future production during the rest of the season and can even effect growth in future seasons Prolonged mismanagement can seriously reduce the useful length of life of a ley, thereby increasing the overhead cost of establishment More often the ley is left to produce at a lower potential for several years and concentrate foods used to make up the deficit

The importance of the palatability of the sward has been repeatedly mentioned and this aspect cannot be overemphasized, particularly so far as the high-yielding cow is concerned Although we can control within quite precise limits where the cow grazes we cannot effectively control what proportion she will consume of the herbage offered Immediately we commence putting on too much pressure in the form of hunger, in an attempt to clean up the rougher herbage, the cow will begin to reduce her intake and in the case of the high producer, milk yields will suffer increasingly (Line, 1960) Thus we can only control the cow to a certain degree, the final choice of what is to be eaten actually resting with the animal

The reaction of the cow on seeing the stockman is a useful indication of the situation When well fed she will pay little or no attention to his approach, whereas at the other extreme she will become agitated and follow him about the field making a good deal of noise in the process Generally a few cows are prone to 'making a fuss' before the rest and these act as a useful guide for future pasture allocation There is in fact a fair amount of time in which to make rationing adjustments before milk yields are seriously disturbed Observation of cow reaction under these conditions is as useful as any other estimate of requirements that can be made Even where an elaborate herbage-sampling scheme is employed in pasture experimentation, quite apart from the considerable time and effort involved there is little indication of the actual percentage of the herbage which the stock can be expected to eat, particularly after the first grazing of the season when the concentration of dung-influenced patches has increased This can only be ascertained with reasonable accuracy by grazing a test area, much as is done in practice when commencing to strip-fold a field

Careful observation of the sward is also helpful for every effort should be made at each grazing to remove all the leaf 'flag' of the plants on the areas not affected by dung from the previous grazings If

attempts are made to force the stock to eat the patches influenced by dung from previous grazings undesirable, very close grazing of the unfouled areas is unavoidable, the tougher bases of such plants apparently being preferred even to the leaf of dung-affected plants. The best that can be done is to 'top-over' with a mower occasionally to remove unpalatable growth. If this is done before the cows have been removed a good deal of the mowings will be eaten, especially if there is little ungrazed herbage to attract their attention. Some animals appear to find such toppings particularly palatable especially when they have dried out a little. Lack of palatability due to the effect of dung dropped during previous grazings presents a serious problem when high-yielding pastures are repeatedly grazed as much as five or six times or more a season. During the later grazings quite a large proportion of the herbage is refused, rank growth being similar in appearance to that produced by heavy nitrogenous dressings. Occasionally the fouling will even survive from one season to the next. Under such circumstances, while the plant nutrients in the dung produce a strong herbage growth, the material so produced in these areas is not utilized to much extent for some time. It is worth mentioning that increased growth due to urine patches presents little problem, the cows often showing a marked preference for the herbage growing on these areas, providing the growth has not been allowed to get too coarse (Nevans, 1941). To reduce the concentration of dung-influenced patches it is much better to contrive to cut some of the crops of herbage and spread out the grazing over as large an area of the farm as possible. Dung-affected patches of herbage from previous grazings will then be removed in the cut crop, thereby eliminating the job of topping-over. After conservation, so far as is known, such herbage is not particularly unpalatable and in any case the concentrate foods normally fed in association with conserved pasture crops will help to buffer any adverse effects. A careful study of the local effects of dung and urine from cattle on the yield and botanical composition of a permanent pasture has recently been published (Norman and Green, 1958). Increasing the grazing area is also likely to reduce the concentration of internal parasites on the herbage, although this aspect is not generally regarded very seriously so far as adult cattle are concerned. The only practical method of herbage feeding which avoids 'dung fouling' of the pasture completely and largely prevents any selection of the sward is 'green soiling' or 'zero grazing'. Disposal of the manure accumulating in the yards where the herbage is fed still poses a considerable problem.

A good deal has been said in the past about plant selection, the animal picking out the more palatable species to their detriment so far as future competition with other plants in the sward is concerned This situation is likely to occur on permanent pastures where there is a fairly large range of species, grazing is more or less continuous and the sward is left for a sufficient number of years for 'evolutionary' changes to occur Such a process on present-day leys is not evident to much extent for there are too few species present in the simple mixtures used and the difference in requirements between the bred strains of grasses is not nearly as marked as it is between the components of a permanent pasture Leys are much less stable than old pasture and it is general management which has the main influence on sward composition in the short term For example, if a Cockle Park mixture is closely grazed or cut frequently the perennial ryegrass and white clover will become predominant. A single high dressing of nitrogen followed by a heavy silage or hay cut will seriously depress the clover and encourage the cocksfoot Animal selection from species to species particularly with intermittent as opposed to continuous grazing, does not appear to play a dominant role The sward should be treated as a single entity to be utilized at intervals as completely as possible and if there is any tendency for the cows to leave a particular species ungrazed this effect can be eliminated by cutting treatments

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CHAPTER ELEVEN

Beef Cattle and Sheep

M. MCG. COOPER

Characteristics of fattening pastures—Fertilizer treatment—Characteristics of sheep and beef cattle production—Adaptation of management practices—Sheep-cattle ratios—Wintering of stock—Sward composition—Diseases and parasites as limiting factors.

Though the herding of sheep and beef cattle on pasture is one of man's oldest occupations, there is comparatively little precise information on the best methods of obtaining maximum profitability or productivity. We do not know, for instance, the most desirable species combinations in relation to soil and other natural conditions, the most efficient systems of grazing nor the correct ratio of sheep to cattle where mixed grazing is practised. Our knowledge is largely empirical and has been built up from centuries of experience to constitute a recognized grazier's craft.

CHARACTERISTICS OF FATTENING PASTURES

Certain fields have local and even national reputations for their fattening qualities, for instance, Snave Corner on Romney Marsh and Millfield in the Welland Valley, but no one has yet distinguished the attributes which place such pastures in a category above adjacent grazings which are rated as having no more than a store function. Generally these fattening fields have fertile, well-drained soils which will sustain growth over a long season. The most important species are perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*), but usually there are appreciable proportions of such species as

the *Poas*, timothy (*Phleum pratense*) crested dogstail (*Cynosurus cristatus*) and browntop (*Agrostis tenuis*) Very often herbs such as yarrow (*Achillea millefolium*) and narrow-leaved plantain (*Plantago lanceolata*) are present and this has led to a considerable amount of conjecture as to the value of such herbs in grassland The comparative thriftiness of livestock on old grassland, in contrast with the fairly common occurrence of metabolic disturbance on leys consisting of simple mixtures, has created a school of thought which believes that the inclusion of herbs in grass mixtures is advantageous There is no scientific evidence to show that higher live-weight gains or healthier or better finished stock can be obtained from pastures containing sown herbs Thomas and his co-workers (see Thomas, Thompson, Oyenuga and Armstrong, 1952) have shown that many of these herb species, notably yarrow, plantain, burnet and chicory, have a very high mineral content, but recently Scoud (1959) has been unable to establish that these species have any beneficial effects on ewes and lambs In fact the pasture which included sown herbs had a lower live-weight output per acre than a similar mixture without herbs or an old permanent pasture with which it was compared It is interesting to note that in this trial there was a considerable build-up of *Nematodirus* infestation over a period of three years The permanent pastures produced lambs with the lowest worm burdens and had the fewest mortalities from this cause, even though rates of stocking were identical

Undoubtedly the quality and the reputation of English fattening pastures is in a large measure due to the systems of stocking which have been adopted Great attention is paid to the equation of pasture growth and stock appetite, so that there is no serious overgrazing or, even more important if a good balance of species is to be maintained, undergrazing, which is one of the besetting sins of pasture management Usually the good management of fattening pastures is at the expense of adjacent store pastures, which are used as reservoirs for stock and suffer in consequence It is possible for the exacting demands of fattening fields to have a detrimental effect on the productivity of farms as a whole

Usually fairly mature stock graze these fattening pastures for it is said that the swards are too 'strong' for young stock such as lambs or yearling bullocks This, of course, is advantageous from the viewpoint of maintaining fertility on what are naturally fertile soils, for the withdrawal of major plant nutrients such as calcium and phosphorus, is trifling compared with that where milking stock are carried The

nitrogen status of soils is abundantly preserved by the maintenance of a strong white clover element in the sward, combined with a full measure of utilization by the grazing animal, whose excrements are so important in maintaining soil fertility (Wolton, 1955).

FERTILIZER TREATMENT

Fertilizers for such fattening pastures are usually limited to occasional dressings of phosphate and lime. Nitrogenous fertilizers are seldom applied. Apart from any prejudice against their use on the grounds of causing unthrifty stock or a lack of clover in the sward, there is the yet unresolved question of their economic worth. Both sheep and beef cattle have a low efficiency of food utilization as compared with dairy cows (Hammond, 1950) and the additional live-weight increase secured from liberal nitrogenous fertilizing may be insufficient to justify the expenditure involved. This certainly was Cornforth's (1955) experience in a trial at Wye College where he compared nitrogen at the rate of 110 lb. N per acre with a control where no nitrogen was applied. The original pasture had a good balance of white clover which was preserved throughout the trial on the control plots. The experimental area was grazed by hoggets and rotational and non-rotational grazing were included as additional treatments. The aim throughout the two years of the trial was to secure full utilization of herbage by adjustments in stocking rates. There was no measurable advantage from applying nitrogen under a non-rotational system, either in respect of total live-weight increase or increase per sheep. The advantage in applying nitrogen under a rotational grazing amounted to 60 lb. of live-weight increase per acre which was 11 per cent more than the output from the no-nitrogen treatment. Individual sheep gains were not as good on the nitrogen treatment nor was the finish of sheep at the end of the trial. Apart from the longer grazing season on the nitrogen-dressed pastures there appeared to be no advantage in using this fertilizer for fattening this class of sheep.

CHARACTERISTICS OF SHEEP AND BEEF CATTLE PRODUCTION

The low efficiency of both beef cattle and sheep in respect of food use necessitates a reliance on cheap feeding stuffs and these animals are consequently better fitted to a ranching system than to an intensive

system of farming Though intensive pasture management with a liberal use of fertilizers and special-purpose leys is commonplace with dairying both in Britain and abroad, it is seldom encountered in either sheep or beef production, because with the more usually adopted grazing techniques and present price relationships the value of production is not usually sufficient to justify the cost of intensification It is true that there is intensive sheep and beef production but this mainly occurs on land which is naturally highly productive, such as very good permanent pasture or long-duration leys Both beef and sheep production is characteristic, therefore, of extensive farming where units are large and land is comparatively cheap Such conditions are found in new countries such as the Argentine, Australia and New Zealand, where the pressure of human population and also the burden of supplementation during periods of pasture shortage are not great (excepting, of course, the drought hazards of Australia, which can be catastrophic) Parts of Britain provide an exception to the general rule that countries with limited land cannot afford the relative inefficiency of beef cattle and sheep on good land Here one is usually concerned with large farms with low rental values, where the occupiers can afford the luxury of low farming and concentrate on the production of fat rather than store stock For the main part in countries with limited land resources, both beef and sheep must be by-products of other more profitable lines of farming, e g utilization of crop residues and of the restorative ley in what is primarily a cash-crop system of land use

This general rule does not apply to land of lower quality in Britain and other densely populated countries especially where there are upland grazings, where sheep either for wool or for stock production, are of paramount importance in utilizing land which is beyond the margin of intensive use The deficiencies of the sheep as a utilizer of food are offset by its capacity to survive and thrive on indifferent herbage As a species it has an advantage of a fairly short gestation period and Wallace (1948) has shown that it is only over the last third of pregnancy that there are likely to be critical demands of the foetus for nutriment Again, lambing takes place just prior to active pasture growth so that the maximum demands of the growing lamb and the lactating ewe coincide with the peak of pasture production As pasture growth fails the lambs are weaned and surplus stock are removed from the hill

Within the species there are breeds which show a high measure of adaptation to such conditions The Merino as a breed is of very great

value under conditions of sparse grazings, especially where the rainfall is low. It is not found under the high-rainfall conditions of British hill-country farming, for these uplands have their own breeds, notably the Scotch Blackface, the Welsh Mountain, the Swaledale and the Cheviot. The last-named is a breed of the green hill as opposed to the black or heather hill, which is the normal habitat of the Blackface and allied breeds.

Adaptation goes further than species and breeds. It extends to actual flocks and there is a recognized 'hefting' value on certain grazings when they are taken over as a going concern. Here the adaptation possibly covers acquired immunity from local infections as well as a knowledge (if that is the word) of the local grazings on the part of the sheep. There is a considerable lore among hill-country shepherds on such questions as the relationship of sheep to their grazing; for instance Welsh shepherds believe that the direction in which off-wintered stock move back to the hill in the early summer influences their ranging habits in the subsequent season (Owen, 1955).

Cattle have, or should have, an important function in the maintenance of quality in upland grazings which are primarily devoted to sheep. Several farmers, notably McGuiness (1947), Bennett-Evans (1949) and Stewart (quoted by Davis and Cooper, 1953) have been able to demonstrate that cattle, used primarily as animate mowing machines, are effective in restoring a predominance of more nutritious bottom grasses which are so important to sheep. McGuiness records that though he reduced the size of his sheep flock when he increased the companion beef herd, nevertheless he increased the output of wool and improved the lambing percentage and the quality of store stock. On Ben Challum in Scotland, Stewart was able to increase very materially the sheep-carrying capacity, the lambing percentage and the quality of the lambs, largely through the agency of a single suckling herd of Cross-Highland cattle.

Bennett-Evans stresses that sheep are the masters and cattle are the tools in hill-country farming. Apart from the fact that sheep produce wool as an additional product for sale, cattle are not so well adapted to sparse grazings, and they will starve where a sheep can survive. Unless farms have cultivable 'inbye' land, wintering becomes a problem because of the necessity for expensive supplementary feeding. In countries like New Zealand, which have relatively short winters, it is possible to winter on a quality of grazing which approximates to 'standing hay', but in Britain, where the growing season on most

uplands is less than five months and where there are also the heavy winter demands of the ewes, this is not practicable If cattle are out-wintered there must be a supplement of hay, a crop not easily conserved on hill farms, which are generally in high-rainfall areas Silage appears to be the logical winter supplement, but it is not a sufficiently mobile source of nutriment to be used other than on the inbye land where it is produced There are in consequence strong arguments for the summer agistment of lowland cattle on the hills and for their return to the lowlands in the winter They may not have the 'rustling' qualities of the genuine hill breeds and crosses, e g the Galloway, West Highland and Cross-Highland, but nevertheless they will do a useful and essential job if they are properly herded

Subsidies of various kinds apart, one cannot expect a great deal of direct profit from cattle kept on the hills Their function, it is reiterated, is the secondary one of removing tussocky or unpalatable grasses such as *Molinia* in order to improve the sheep-carrying capacity of upland grazings

On the larger grassland farm between the hills and the intensively cultivated land both sheep and beef cattle play an important part in the utilization of grassland Here their low food-conversion efficiency is offset by the high measure of labour efficiency that can be obtained In no sense can the grassland management be termed intensive Generally the grazing areas are large and fertilizers are used sparingly The primary aim is to get a sward with a reasonably proportioned clover element, for such farming does not warrant the use of nitrogenous fertilizers except to provide a limited amount of early grass for lambing ewes or for stimulating the hay crop It is good farming practice to apply both phosphate and lime where these are required Either permanent grass or long-duration leys are employed, and though such species as ryegrass timothy and cocksfoot may be sown originally, along with white clover, there is a tendency for regression to the *Poa* and *Agrostis* species and Yorkshire fog

Normally non-rotational grazing is practised, certainly with ewes and lambs and with fattening cattle, because it is generally held that better finish is obtained if such stock are not disturbed by movement This point, which will be discussed in more detail later, applies also in more intensive sheep or beef production. Store cattle however, may be moved from field to field in order to keep pastures in balance The aim with sheep pastures, is generally to maintain a short dense sward and the store cattle are used to attain this end Again in this, as with

the management of fattening pastures, there is a tremendous grazier's skill and a good manager will be able to ring the changes in stocking, along with a limited use of the mowing machine, to secure the sort of sward he requires. Sometimes the management of the sward will have to be sacrificed for the welfare of the stock, e.g. in drought periods there may be severe overgrazing, but the essence of success in such farming is a maintenance of a practical compromise between the sometimes conflicting demands of stock and sward.

With breeding ewes, the farmer is fortunate that there is a period between weaning and about three weeks before mating when, in their own interests, or rather in those of the subsequent lamb crop, the ewes should be kept on short commons. This provides an opportunity, of about two months' duration, when the ewes can be used to eat out, field by field, the rough growth which may have been neglected during the main grazing season. In this way it is possible to bare the herbage so that favourable conditions for shade-enduring weed species are removed. Also the plant nutrients locked up in such herbage are returned as dung and urine and promote further new growth. Deterioration of pasture can be arrested by such treatment in the late summer and there will be a fresh growth in the autumn flush.

This mowing function of sheep makes them particularly valuable on the dairy farm as a tool for grassland management. Invariably on such farms there are fields which in the late summer appear as a mosaic of long and short growth due to the fact that dairy cows avoid herbage that has been fouled with their excrements. Fortunately sheep, when they are hungry, will graze closely to dung patches and achieve a defoliation which obviates the need for mowing. After mating, when active pasture growth has ceased, they may be used again for this same purpose. When sheep are used in this way it is important that there is good fencing so that the flock may be securely concentrated on a given area. It is equally important that the flock size should not be so great that the early spring bite for the dairy herd is prejudiced. On farms used primarily for dairying, sheep must be complementary to and not competitive with the dairy herd.

ADAPTATION OF MANAGEMENT PRACTICES

Turning now to systems of grazing, it has already been stated that most sheep farmers prefer set stocking for both bullock fattening and fat-lamb production because it is claimed that better finish is obtained.

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There is a certain amount of experimental evidence to support this view. A trial at Ruakura in New Zealand (N.Z. Department of Agriculture, 1953) investigated both rotational and non-rotational, or 'set', stocking at two levels, namely four ewes and their lambs and a half cattle beast to the acre, and eight ewes with lambs to the acre. The conclusions were that at the lower rate of stocking, non-rotational grazing gave lambs of higher live and dead weight and of better finish, while the gains in cattle, which were used to control growth at this lower rate of sheep stocking, were also higher. Rotational grazing gave the better live-weight gains, carcass weights and grades at the higher rate of sheep stocking. It was concluded that rotational grazing was likely to be of most value to farmers adopting high rates of stocking with ewes but using no cattle.

Thompson and Hooper (1952) compared set and rotational stocking of lambs on a ryegrass/subterranean clover pasture in Tasmania, and the former method showed significantly the greater gains. The growth rate of the rotationally-grazed lambs showed a greater slowing down, as maturity was approached. A rigid four-week rotation was adopted and this may have been responsible for the difference, for with such a time lag at certain stages of the pasture growth cycle, herbage could become over-mature for ewes and lambs.

Similarly, in another Australian trial (Moore, Barrie and Kipps, 1948), no advantage was obtained from rotational as opposed to continuous grazing of 'a stabilized pasture mixture'. It was considered that provided the pasture satisfied the energy requirements of the animals, continuously grazed swards are as productive as those rotationally grazed. In fact rotational grazing was thought to be an advantage only where the stocking rate fluctuated to allow the consumption of herbage to equal its growth rate.

Cornforth (1955), in the work already referred to, obtained a 23 per cent advantage for rotational over non-rotational grazing on the pastures that received 110 lb. of nitrogen. On the pastures that did not receive fertilizer nitrogen the difference amounted to only 10 per cent more live weight per acre from the rotationally grazed pastures.

The Australian results, and to some extent those from New Zealand, are disappointing in view of the classical work by Woodman and his associates on the effect of intervals between defoliation on the production of nutrients from pasture. It is also in conflict with Levy's (1949) opinion that rotational grazing gives a fifty per cent greater

productivity than non-rotational grazing. Unfortunately one is denied the essential information about the various experiments to form an independent judgement. As the Ruakura work has shown, intensity of stocking is important and the highest live-weight gains per acre were obtained from rotational grazing, using eight ewes and their lambs per acre. It is possible that in both the Australian experiments there may have been a measure of under-utilization which not only prevented rotational grazing showing to best advantage, but also may have resulted in a deterioration in the quality of herbage available to the sheep. There is a tendency with set stocking towards a pattern of long and short grass and from the latter sheep would continue to obtain some good-quality herbage. Where a rigid time interval is fixed between grazings, the results of rotational grazing experiments are more easily analysed statistically, but tend to have more restricted application. Farmers who successfully practise rotational grazing with sheep insist on making the movement suit the needs of stock and pasture, thereby avoiding over-mature pasture and using the mowing machine for the conservation of surpluses.

There is a definite management advantage from rotational grazing under farm conditions in that it gives this flexibility for conservation of surpluses. Under set stocking where the fields are large, surplus grass tends to be spread in neglected patches over the whole grazing area. This is a point of considerable concern in a country such as Britain where there is a problem of building up sufficient food reserves for a long winter. The same result can, of course, be obtained under set stocking if there is sufficient subdivision to permit 'bunching-up' and withdrawal of fields from grazing.

Though under optimum conditions high live-weight increases per acre can be obtained from rotational grazing (e.g. Davis and Cooper, 1953, report live-weight increases from lambs and hoggets exceeding 900 lb. per acre annually), it is generally agreed nevertheless that there is some sacrifice of finish in the animals so grazed as compared with those set-stocked at rather lower concentrations. This may be due to a disturbance of stock, either in their movement from one area to another—a point which is likely to be serious with young lambs due to temporary mismothering—or through an upset in the rhythm of grazing. Pendrill (1952) observed, for instance, that hoggets spent a significantly longer period grazing or searching for food on the fourth day in a field as compared with the second day. Where movement of stock takes place at intervals of 4 or 5 days, there are fluctuations to give

a saw-tooth effect to the graph of the plane of nutrition At the beginning of a grazing period there will be an abundance of good feed, but immediately prior to a change sheep will be forced to eat poorer herbage This may be critical with suckling lambs, for a weight difference of only 3 or 4 lb at weaning may make an important difference in grade The danger of forcing fattening stock too far in the interests of full utilization can be obviated to some extent by the use of 'follower' stock, which have lower nutritional demands, e g dry sheep intended for breeding or store cattle

W R Merricks, a Sussex farmer, devised such a system in 1953, when he subdivided 55 acres of a good ryegrass/white clover pasture into ten grazing units, which were grazed on a rotational system of 3 days fattening cattle, 3 days fattening sheep and 3 days store sheep, followed by 21 days' rest The final result was that rather more than one cattle beast and five sheep per acre were fattened and five additional sheep, intended for breeding, were summered in a forward condition The total live-weight increase per acre, over a period of six months, exceeded 600 lb The cattle tended to scour a little on the lush grass and perhaps did not have the finish of set-stocked cattle on comparable pastures, but nevertheless they had the condition to suit modern market demands

A development of considerable topical interest is a system of forward 'creep' grazing of ewes and lambs which has been devised at Cockle Park (Dickson 1958) It has been noted by several workers, e g Wallace (1948), Barnicoat, Logan and Grant (1949) and Labban (1956), that the suckled ewe reaches a peak in milk production in 2–4 weeks from parturition Thereafter yields tend to fall and at the 8th–10th week may approximate to half the peak level Labban found that there was a strong positive correlation ($r=0\ 9$) between milk yield of ewes and live-weight gain of lambs from birth to 8 weeks From 8–16 weeks the condition was small and not significant It seems that just at the point where the lambs' appetites are increasing the ewes' efficiency is decreasing and they are in fact becoming highly competitive with their lambs for available grass

One device occasionally adopted to meet this situation is the weaning of lambs at 11–12 weeks to give them preferential grazing This procedure has two disadvantages The first is that it denies lambs a small amount of milk which has some value for them and the second is that ewes which are weaned early tend to get very fat The Cockle Park system was designed to avoid these two difficulties The grazing area

is subdivided into six paddocks and creep access is provided for lambs from one paddock to the next in the grazing rotation. At all times during the suckling period the lambs have access to fresh grass and so they are able to give full expression to their growth potential. Early in lactation the ewes are not required to graze closely, but as the season advances and there is a parallel deterioration in their milking ability and in the quality of the herbage, they assume more and more the function of scavengers behind their lambs.

Under experimental conditions with five ewes and ten lambs per acre, creep grazing showed an advantage of 11 lb. per head within a period of 14 weeks over lambs that were on conventional rotational grazing where ewes and lambs were run together. The difference in weight was reflected in condition for 85 per cent of the creep lambs were judged to be fit for slaughter as against 38 per cent of the rotationally grazed lambs.

The observed differences were attributable not only to superior nutrition but also to lower worm burdens as measured by faecal egg counts. It seems that the lambs were ingesting herbage carrying less infective larvae and possibly ewes following behind, with their age tolerance, were acting as disinfecting agents.

Forward creep grazing has been tested on a commercial scale using flocks of approximately 200 ewes with their lambs and the experimental promise of the system has been fully maintained. There has been no evidence of mismothering and it has been possible to achieve rates of stocking of 7–9 ewes and 10–14 lambs to the acre with the majority of the lambs being sold fat off thin mothers at more than 40 lb. dressed weight. In one such commercial trial at Nafferton Farm, King's College, Newcastle-upon-Tyne, 630 lb. of live-weight increase were obtained in 14 weeks.

Spedding and Large (1959) have been investigating an alternative form of creep grazing where lambs have access to a pasture alongside the area reserved for the ewes and precautions are taken to prevent the lambs going back on to pasture carrying a contamination of the infective larvae of endoparasites. They have obtained outputs corresponding to those that have been reached with forward creep grazing. Though there are differences in techniques as between the two systems they embody the same principle of giving preferential treatment to the lamb at a stage when it is capable of making high rates of gain and a very efficient use of food. As a consequence it makes intensive fat-lamb production a reasonable alternative to dairying on

medium-sized grassland farms providing always that the problem of economical winter feeding of the ewe flock can be resolved

The principle of preferential grazing for young stock has been followed for a number of years at Ruakura Animal Research Station in New Zealand (N Z Department of Agriculture 1953) Over a period of nine years rotationally-grazed Jersey calves at 8 months have averaged 396 lb as compared with 291 lb for calves which have been set-stocked This difference has been caused by running the young stock on fresh grass in advance of the milking cows McMeekan (1954) reports that though the rotationally-grazed calves had worm burdens their thrifty condition enabled them to withstand the effects of parasites The benefit of rotational grazing is maintained in the second year for the rotationally-grazed heifers at 20 months averaged 150 lb more than their set-stocked mates and this is a substantial difference for Jerseys of this age

This New Zealand work in the rearing of young stock has a particular interest for Britain at the present time in view of the efforts which are being made to increase the output of beef from calves which are obtained from dairy herds Unless autumn- and winter-born calves are weaned on to dry food at an unusually early age (Preston, 1956) the high price of whole milk in winter makes their initial rearing expensive With conventional feeding the successful exploitation of grass in the following summer can be a valuable offset to the heavy costs of winter feeding Hamilton (1956) has shown that grass is quite the cheapest form of nutriment available for stock on British farms and economically it is important to exploit this fact especially with stock such as beef cattle which have a low efficiency of food conversion.

SHEEP-CATTLE RATIOS

Turning to the question of ratios of sheep to cattle in a mixed stocking system it is popularly held that a combination of the two gives a more efficient utilization of pasture than the use of one species alone Unquestionably this is true on upland grazings where mechanical methods of controlling the balance of the sward are denied the farmer The position may be different on lowland farms where the mowing machine may be used and closer subdivision makes possible a more intensive concentration of sheep at critical times In a trial at Ruakura (Report of N Z Department of Agriculture, 1954) three rates of stocking have been compared, as follows

(1) Four ewes per acre, with lambs, plus $\frac{1}{3}$ cattle beast per acre wintered and fattened.
(2) Six ewes per acre, with lambs, plus $\frac{1}{3}$ cattle beast per acre bought in the spring and fattened.
(3) Eight ewes, with lambs, and no cattle.

Over three years meat production on all three systems was virtually identical at approximately 250 lb. per acre, but the 6-ewe level produced 42 per cent more wool and the 8-ewe level 86 per cent more wool than the 4-ewe level of stocking. There were no real differences between the three systems in vital statistics for either ewes or lambs. Relative to the 4-ewe level, 6 ewes showed an increased cash return of $12\frac{1}{2}$ per cent and 8 ewes an extra return of 25 per cent as a consequence of the greater value of lamb relative to beef, and the increased wool production at the higher sheep-stocking rate. These results conflict with those given in annual reports from the Cockle Park Station. There, cattle and sheep together gave twice the live-weight increase per acre that was obtained from a corresponding manurial treatment where only sheep were grazed. The author's view is that this result should be viewed with some scepticism. The areas compared were unequal in area and there was no replication except in time. Furthermore, the observations extended over a period of only 14 weeks and the rate of stocking on the sheep-only treatment was low. If sheep-stocking rates had been doubled a different result might have been obtained. This draws attention to the importance in grazing studies of having as one variable the intensity of stocking, for as the Ruakura work on set versus rotational grazing in sheep, has indicated, intensity of stocking may show some interaction with the systems of grazing (or manuring of pasture) which are being studied.

The whole question of sheep–cattle ratios is now being investigated at the Husbandry Farms of the Ministry of Agriculture, Fisheries and Food. A comprehensive plan is being followed and there will be replication on each farm as well as replication in time and in district. This is important, and variations in soil or climatic conditions may profoundly affect results. For instance, it is conceivable that where there are serious local infections of *Nematodirus*, cattle may be advantageous because they dilute the rate of stocking with susceptible animals and there may possibly be some ingestion and destruction of infective larvae by cattle. This has long been held to be one of the functions of cattle in a mixed grazing system, though the availability of effective anthel-

munities for round worms has reduced the cogency of this argument. There still remains the other possible argument in favour of mixed grazing, namely that cattle control the pasture so that it is more suited to sheep, but there are farmers who practise 'gang-mowing' to preserve the lawn-like sward. There has been no satisfactory experimental work done to establish the efficacy of gang-mowing, but trials are now being undertaken at the Ministry Husbandry Farm at Drayton near Stratford-on-Avon. The author conducted a limited trial on gang-mowing with set-stocked sheep and obtained small but inconclusive advantages from it. One deprecates, however, a mechanical system of pasture control as a regular practice if equally good results can be obtained by using cattle, which derive benefit from the food they ingest.

Like sheep graziers, cattle graziers do not favour rotational grazing, but generally prefer to adopt a non-rotational system to put the best bloom on their cattle. Very little experimental evidence is available on this point, though Davies and Williams (1948) in their study of the production of permanent pastures compared with temporary leys, recorded their highest live-weight gains on a farm which practised rotational grazing. Because this work was not replicated, however, only surmises can be formed. The objections to rotational grazing that are usually advanced are those of disturbance, but very high rates of gain for rotationally-grazed cattle have been obtained at the Grassland Research Station, at Hurley. There is little evidence on the value of strip-grazing, using the electric fence, for fattening cattle. A number of farmers have tried the system, but there has not been the widespread adoption that has been experienced in dairying. On the one hand it seems that, as in dairying there would be a more efficient use of grassland, but on the other there is the counter of a great deal more labour and attention. Cattle feeders are traditionally 'dog and stick' men, with a large number of acres at their disposal and, unlike the smaller-scale dairy farmer, without the same urgency to make the most out of a small area of land.

One farmer who tried the system admitted to the author that he increased his carrying stock capacity, but that his stock were restless, especially when they were given their first break in a field. Furthermore, he did not get the finish on his stock that he obtained with conventional grazing, which with the existing grading system, introduced a price penalty. Today, with a free market, the butcher's preference is for leaner stock and this objection may not be quite so valid. It is unfortunate that the manifest advantages of strip-grazing

for dairy cattle cannot be repeated for beef animals in a country where beef is still in such short supply, but so far as fattening cattle are concerned the method seems to have little appeal.

WINTERING OF STOCK

The wintering of store cattle on good foggage is a rather different proposition, for in the winter months, with uncontrolled grazing, spoilage can easily exceed the quantity of utilized grass. In this connection the system of growing cocksfoot and lucerne in alternate rows, devised by Hughes (1950) at the Grassland Research Station at Drayton, is worthy of mention. He applied a heavy dressing of nitrogenous fertilizer to his swards in August to promote a vigorous growth of cocksfoot in the autumn, and thus to provide a quality of keep which was at least equal to average-quality hay, and which was capable, with rationing, of maintaining stores in good condition over the winter. The cattle walked the rows of lucerne, which died in the winter, and in this way minimized treading effects on the cocksfoot. The lucerne was not impaired by this treatment and came away vigorously in the following spring. This alternate-row system seems to be particularly valuable on heavy land, and with back fencing to give protection to the sward there is a particularly good recovery of the cocksfoot and poaching is minimized.

Out-wintering of bullocks is a good practice, provided it can be done without detriment to the sward, not just because it lowers the cost of wintering but also because it obviates the check and loss of condition characterizing in-wintered bullocks when they are turned out to grass. It is not known whether this check is due to changes in the rumen flora, or to a combination of this and other factors. Whatever the cause may be the check is a real one, and for this reason graziers pay more for bullocks with rough coats and mud on their legs, obvious signs of out-wintering, than they do for animals that have enjoyed a less stringent winter in yards. Where it is essential to in-winter stock it is important to make the transition to spring grazing a gradual one by putting them in a relatively bare field with some shelter, and to continue part of the winter feeding regime until such time as the stock wean themselves off supplementary food on to the young grass as it increases in quantity. The principle of gradualness in change is a very important one in stock management.

SWARD COMPOSITION

Relatively little is known about the optimum sward composition for fattening stock Obviously it is important to have associations which have a long growing season produce a high quantity of dry matter per acre and preserve a good ratio of leaf to stem These conditions are best satisfied by a sward which contains a high proportion of perennial ryegrass and white clover but there may be other species which are important too It is safe to say, however that swards which are dominated by *Agrostis* species or Yorkshire fog have too short a growing season and too low a production of digestible nutrients to satisfy the conditions of a good pasture It was remarked at the outset that certain fields in Britain have achieved reputations for fattening and others for growing stock without putting on condition but no one has been able to define with certainty the essential differences between such pastures During the wartime ploughing up campaign, the owners of fattening fields maintained that the intrinsic virtue of their pastures would be irrevocably lost were they to be ploughed The Royal Agricultural Society sponsored a series of trials comparing leys and permanent pastures and these have been reported by Davies and Williams (1948) The results produced no evidence that even the best permanent pastures had qualities which were lacking in well-managed leys

In the author s experience cocksfoot is not a good species for promoting live-weight gains or finish if it is a dominant element in the sward Certainly it is high yielding but it is not a particularly palatable grass It is a species which ss widely included in long ley mixtures which are used for both cattle and sheep but there has been little critical work to determine the comparative value of cocksfoot or of any other species There is room for this in grassland experimental programmes

DISEASES AND PARASITES AS LIMITING FACTORS

One interesting point on the value of white clover for fattening lambs emerges by accident from some work in New Zealand concerned with a study of a photosensitive condition known locally as facial eczema Very often following summer droughts there are warm rains which promote very rapid pasture growth especially of ryegrass Such lush growth carries some principle which causes a liver disfunction of which the eczema is a secondary condition A trial was

laid down which included swards with a dominance of white clover in the hope that they might constitute safe pastures. They were grazed normally by ewes and lambs in the spring and summer, and it was noticed that better lambs were drafted from these clover-dominant swards than from normal grass-clover mixtures.

This result is strangely in conflict with a widely held view among sheep farmers in the north of England who do not favour a high proportion of clover in their fat-lamb swards. There is a prejudice against the use of basic slag on this account. It is not known whether there is any real substance to this dislike of clover dominance, and there are no definite grounds advanced to explain the situation. One suggestion is that the trifoliate leaves provide a particularly good micro-climate for the survival of the infective larvae of round worms.

Seoud (1959) has investigated this point in a comparison of a clover-dominant as opposed to a ryegrass-dominant ley, grazed by ewes and lambs. In the first year of the trial the lambs on the clover leys made better live-weight gains, but their advantage was not significant. In the second year of the trial both the swards carried a high level of *Nematodirus* spp. There were more clinical cases of Nematodiriasis and more mortalities on the clover-dominant sward.

Pasture, unfortunately, is more than a source of nutrient for the stock it carries, it is also an environment and may carry infections or be responsible for imbalances which may influence the health of stock. Fortunately one major problem in the grazing of certain pastures has been resolved, namely deficiencies in the trace elements, cobalt and copper. Large areas of grazing, deficient in one or other of these elements, have been made safe by appropriate top-dressing or by the provision of mineral supplements. Fortunately most parasitic round worms can be controlled by modern anthelmintics, of which the most notable is phenothiazine. Lung worms causing husk or hoose in cattle, and also afflicting sheep, are now being brought under control, though the best protection is avoidance of trouble by both the provision of clean grazings—and here mixed stocking and change of grazing are valuable—and the provision of good feeding, so that stock may be better fitted to withstand infections. To give this protection to lambs it may be necessary to provide a small ration of corn. Young cattle are particularly susceptible to husk, and its ill effects, and on some farms it may be necessary to yard young stock early in the autumn and allow them access only to dry grass, e.g. after the dew has passed. Serious trouble is not normally encountered where rotational grazing

on the Ruakura pattern is adopted, i.e. the weaner calves are moved frequently on to fresh pasture and infection is not permitted to build up because of undue concentration of susceptible stock.

The round worm *Nematodirus*, which is responsible for losses in lambs in parts of Britain and in other countries, has already been mentioned. Fortunately there is now a specific, bephenium embonate, which will deal with this worm, but the cheapest and best control will be effected by management. Thomas (1956) has established that, unlike the eggs of most other round worms, those passed by infected lambs do not hatch within a few days to provide further infection, but overwinter and hatch in the following spring. On infected pastures there is normally a peak of infective larvae in the mid-spring period, followed soon afterwards by a peak in the passing of eggs by infected lambs. There is also evidence of a strong age tolerance so that ewes are not a serious source of infection. In other words, the primary source of infection for lambs is the previous season's crop of lambs. Current work at Cockle Park is showing that control by management is possible simply by making a break in the cycle of infection. New leys do not carry infection nor will fields which did not carry susceptible stock in the previous year. Control, therefore, involves an alternation of fat-lamb pastures from year to year and creep grazing now gives the means of concentrating the fat-lamb flock on a small clean area to avoid infection being spread all round the farm.

A variety of other diseases also affect sheep and cattle on pasture, and the most serious of these are the so-called metabolic diseases which include pregnancy toxaemia, hypomagnesaemia and hypocalcaemia. The maintenance of the plane of nutrition over the last weeks of pregnancy appears to be critical in the control of the first-mentioned disease, but low values for serum magnesium and calcium are a more difficult problem. As yet no certain method of prevention has been established and the incidence of hypomagnesaemia is sometimes embarrassingly high on vigorous early-growing leys. In the absence of better knowledge it seems that a sheep farmer who is encountering such trouble is advised to continue supplementary feeding even when there is apparent plenty of grass until such time as it becomes more mature. Quite possibly, as with dairy and single suckling cows, a magnesium supplement such as magnesite may give some control (Allcroft 1954), but this has not yet been definitely established (see, however, Chapter 24).

Fortunately fattening cattle do not seem to be so prone to disease as dairy cattle. Possibly this is in part due to the fact that the former are

not subject to such intensive management or to the same physiological strains as lactating cattle. The breeding ewe, the lamb and the hogget over its first winter are, however, subject to considerable grazing hazards, including, in addition to those already mentioned, infections due to anaerobic bacteria of the *Clostridium welchii* group, e.g. pulpy kidney and lamb dysentery. We are fortunate, however, in the considerable progress in veterinary science, which has provided effective vaccines. One does not accept now that loss under intensive management on pasture is unavoidable, for there are now many pharmaceutical and management aids at our disposal and these will increase with the progress of knowledge and the achievement of a greater understanding of the relationship of the grazing animal to its environment.

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CHAPTER TWELVE

Non-Ruminants

D. E. EYLES

Factors affecting herbage consumption, rations at pasture, effect on health and on animal products, conclusions—Types of sward—Conserved grassland products: green herbage, dried herbage, hay, silage, leaf-protein extracts—Integration of pigs and poultry—Turkeys—Geese.

The main discussion in this chapter is confined to the utilization of grassland by domestic fowls and pigs, which are referred to collectively as non-ruminants. The grazing of turkeys and geese is considered in separate sections at the end of this chapter. All of these animals obtain nutritional advantages from being kept out-of-doors in addition to any benefit derived from actually eating herbage. In Great Britain, except in adverse weather, they receive sufficient sun on their bodies during the summer to produce vitamin D to meet their requirements (Halnan, 1948; Braude, 1954). They have access to soil which is a source of minerals and of other factors similar to the animal protein factor (Cunha *et al.*, 1949) and can eat soil fauna, so obtaining animal protein, although a quantitative estimate of the value of this contribution has never been made. As a result of microbiological activity their dung also becomes a source of vitamin B_{12} (Smith, 1951). All of these advantages can be obtained by keeping non-ruminants on bare soil; therefore, the use of grassland can only be justified if its consumption results in either an improved production or an economy in the use of concentrates (Heuser *et al.*, 1945; Boden, 1952).

FACTORS AFFECTING HERBAGE CONSUMPTION

Both pigs and poultry prefer to graze legumes rather than grasses, and young leaves are selected in preference to old leaves and stems; free

range allows more selective grazing than close-folding and more herbage is eaten (Eyles and Cowlishaw, 1957, Eyles and Alder, 1955) Like cattle and sheep, non-ruminants will graze less if offered concentrates without stint than if these are restricted, and it has been claimed that the feeding of concentrates low in protein encourages grazing and those deficient in minerals encourage scratching and rooting of the soil (Heuser *et al*, 1945, Robison, 1935)

Poultry eat a smaller percentage of their total dry matter intake in the form of herbage than do pigs During the first few weeks of the life of a non-ruminant herbage consumption is negligible, but it increases with advancing age until the animal is mature (Buckner *et al*, 1937, Ballinger, 1943) A maximal herbage intake may not be desirable in all cases since a bulky diet may not contain a sufficient density of digestible nutrients (Cowlishaw and Eyles, 1958) It has been shown that a high herbage intake tends to decrease the egg production of fowls (Temperton and Dudley, 1943) Similarly a large percentage of herbage in the diet of non-ruminants reduces growth rate (Heuser *et al*, Smith *et al*, 1950), hence fresh herbage is of little use for rapidly fattening animals such as broilers With bacon pigs and animals being reared for laying or breeding all of which require a slower growth rate than the maximum, large amounts of herbage can be fed successfully

Because of the influence of these factors and the difficulty of direct measurement, the amounts of herbage ingested by non-ruminants while grazing are not known accurately The value of figures for the consumption of cut green herbage is reduced because these do not take into account selective grazing In the light of the limited data available (Eyles and Cowlishaw, 1958, Eyles, 1959), it may be assumed that the percentage of the daily dry-matter intake that may be provided by fresh herbage is for chicks 5 per cent, for growing and laying poultry 10 per cent, for weaned pigs and lactating sows 10 per cent, for bacon pigs and pregnant sows 30 per cent These figures have been used as a basis for Tables 12 1–12 5, which show the calculated percentages of the individual nutrient requirements which it is estimated are supplied by herbage for each class of grazing non-ruminant stock It will be realized that the figures in these tables are theoretically calculated and can therefore only serve as an approximation In many respects the requirements of breeding hens are similar to laying hens and therefore the former have been omitted from the tables

In every case herbage contributes a large proportion of crude fibre

undigested lengths of herbage Although pigs and poultry are much less efficient at digesting crude fibre than ruminants, they digest the crude fibre of young herbage better than that of cereals (Halnan, 1949, Forbes and Hamilton, 1952) When high-fibre rations are fed to growing non-ruminants their digestive tracts enlarge to accommodate the extra bulk (Sampson and Mussehl, 1936, Bohman *et al*, 1955) Besides containing a lower percentage of crude fibre than mature grass,

TABLE 12.3 *Percentage of total nutrient requirements supplied by very young grass by high-quality lucerne meal and by white claver when eaten at rate of 5 per cent of total dry matter intake of chicks**

Nutrients†	Very young grass§	Good-quality lucerne meal**	Young white clover††
Fibre‡	13	14	11
Total protein	6	5	7
Calcium	—	9	7
Phosphorus	—	2	4
Potassium	—	—	54
Manganese	—	6	28
Iron	—	98	84
Copper	—	39	—
Magnesium	—	—	47
Vitamin A	1 400	420	—
Thiamin	34	19	—
Riboflavin	43	28	—
Pantothenic acid	6	22	—
Niacin	16	7	—
Pyridoxine	21	—	—
Biotin	14	—	—
Vitamin K_1	5 000	—	—

* Heavy breeds 7 wks old 0 5 lb live weight 28 2 gm D M /bird/day
† Requirements according to National Research Council (1954) except fibre
‡ Crude fibre level 7 0 per cent (Ewing 1951)
§ See Table 12 2 note**
†† Analysis according to Morrison (1949)
** See Table 2 12, note ††

young quickly-grown herbage contains more unlignified cellulose which poultry may digest a little and which pigs can digest well (Woodman and Evans, 1947) Thus to obtain the maximum benefit from grazing, only young herbage with a low fibre content must be offered to non-ruminants (Table 12 1)

Reference to Tables 12 1, 12 4 and 12 5 shows that although herbage is an excellent source of vitamins it is a poor source of energy, and

therefore supplementary meal rations must have high energy values and low fibre contents (Cowlishaw and Eyles, 1957). This is normally achieved by using a high proportion of cereal grains. In general, herbage supplies inadequate amounts of calcium and phosphorus for all classes of poultry and pigs (Tables 12.1, 12.2, 12.3 and 12.5). These elements together with salt are best provided by a mineral supplement

TABLE 12.4. *Value of very young herbage to different classes of pigs*

Class of pig	Herbage eaten as % of total dry-matter intake	% of total nutrient requirements supplied by very young herbage‡‡		
		Total dig. nutrients**	Crude protein**	Crude fibre††
Weaned pigs*	10	7	15	30
Bacon pigs†	30	21	58	65
Pregnant sows‡	30	21	50	46
Lactating sows§	10	7	17	15

TABLE 12 5 *Percentage of total nutrient requirements of pigs supplied by very young grass and by medium-quality lucerne meal*

Nutrients§	Weaned pigs*, herbage as 10% of intake		Bacon pigs†, herbage as 30% of intake		Pregnant sows‡, herbage as 30 % of intake	
	Very young grass††	Medium-quality lucerne meal‡‡	Very young grass††	Medium-quality lucerne meal‡‡	Very young grass††	Medium-quality lucerne meal‡‡
Total digestible nutrients	—	4	—	13	—	13
Crude protein	14	11	56	45	48	38
Crude fibre**	36	—	69	—	49	—
Calcium	—	26	—	93	—	85
Phosphorus	—	6	—	25	—	21
Carotene	5 900	1 200	10 000	2 000	2,200	430
Thiamin	98	30	290	89	290	89
Riboflavin	100	73	310	220	260	180
Niacin	58	30	210	110	210	110
Pantothenic acid	10	35	33	120	33	120
Pyridoxine	83	—	—	—	—	—

* See Table 12.4 note*
† See Table 12.4 note †
‡ See Table 12.4 note ‡
§ Requirements according to National Research Council (1953) except fibre
** See Table 12.4 note ††
†† Analysis according to Elvehjem and Sober (1943)
‡‡ Analysis according to National Research Council (1953)

pigs and pregnant sows (Tables 12 4 and 12 5) may receive about half their protein needs from herbage, but poultry obtain a smaller proportion than this

Tables 12 2, 12 3 and 12 5 show that there is abundant carotene in young herbage to meet the requirements of all classes of non-ruminants for vitamin A (Bethke *et al*, 1927, Eyles and Cowlishaw, 1959, Dunlop, 1935) Riboflavin, the member of the vitamin-B complex likely to be lacking in cereal rations, is usually found in young herbage in sufficient quantities to prevent a deficiency except in the case of young chicks Although not supplying the whole of their needs, herbage contributes useful amounts of the other members of the vitamin-B complex to poultry diets (Tables 12 2 and 12 3) and to those of weaned pigs For bacon pigs and pregnant sows, herbage will supply all the thiamin and niacin that is required (Table 12 5) By consuming 5 per cent of young grass, chicks obtain approximately fifty times more

vitamin K than they require (Table 12.3). The percentages of carotene, thiamin, riboflavin and niacin in herbage are highest at a young stage of growth and then decline with increasing age (Kohler, 1944).

Table 12.3 shows that chicks receive appreciable percentages of their requirements for potassium and the trace elements (manganese, iron, copper and magnesium) from herbage. Bearing in mind the chances of soil contamination of herbage it seems possible that non-ruminants eating larger amounts of herbage will obtain most of their trace element needs from herbage.

From the evidence so far presented it can be concluded that when non-ruminants graze dense young herbage an economy is possible in the provision of vitamin and protein supplements. The saving is much less, and may disappear entirely during winter or in a drought. Provided good grazing is available, mashes based on cereals plus minerals may be used successfully to supplement the diets of growing pullets (Heuser *et al.*, 1945; Eyles and Cowlishaw, 1959) and laying hens (Shaw and Nightall, 1951). However, it has been found that the addition of a protein concentrate may be advantageous to grazing poultry, in particular to laying hens (Thomas, 1937). Grazing pigs, from weaning to 100 lb. live weight, need less protein supplement, added to a ration of cereals plus minerals, than those kept indoors (Lassiter *et al.*, 1955). If herbage is plentiful, protein concentrates need not be added to a cereal plus mineral ration for pigs of 100–200 lb. live weight (Morrison, 1949). Evidence, in Great Britain, is incomplete for sows at pasture, but probably their ration should contain animal protein in addition to cereals plus minerals for the last few weeks of pregnancy and during lactation (Morrison, 1949). During early pregnancy the protein supplement can be reduced if ample young herbage is available.

Chicks and sucking piglets from 0 to 8 weeks of age consume little herbage, therefore their concentrate rations must be nutritionally complete. The only possibility is a saving of the vitamin-A supplement. The great advantage of giving sucking piglets access to grassland is that they are less prone to anaemia than piglets kept indoors, because they obtain ample iron from the soil and herbage (Venn, McCance and Widdowson, 1947).

Instead of using herbage to replace specific nutrients in a meal ration fed to appetite as discussed in the previous section, grazing may allow a reduction in the total intake of a balanced ration. When used thus, herbage may act as a diluent to the mash so that the latter is more efficiently digested and absorbed (Duckworth, 1954). As a safety

measure practical feeding scales are sometimes placed at higher levels than the scientific requirements Hence the feeding of less than the practical scale may still supply adequate nutrients It has been argued that this is the reason for the apparent saving of meal when at pasture, but research suggests that young herbage is of direct nutritional value However, mature herbage is not so valuable (Buckner *et al*, 1945, Wallace, 1943) and neither is grazing during winter (Godfrey and Titus, 1934, Davidson, 1930)

During the first few weeks of life of the non-ruminant the provision of grass will not produce any saving in the quantity of meal consumed Reductions of from 7 to 17 per cent can be made in the quantity of meal fed to growing pullets on good pasture compared with those on bare range (Heuser *et al*, 1945), but a greater reduction usually retards growth and the onset of sexual maturity (Vondell, 1943) With laying hens on good pasture from 5 to 10 per cent of meal can be saved by not opening the self-feed hoppers before mid-day and thus encouraging the birds to graze (Eyles and Cowlishaw, 1957) However, a drop in egg production and moulting will occur if birds do not have free access to a supply of mash after consuming herbage (Temperton and Dudley, 1943)

Feeding pigs on the 'Lehmann system' allows an increasing percentage of grass in the total daily intake as the pig grows older Because its ability to digest fibre improves with increasing body weight (Nordfeldt, 1954) the older pig can deal more efficiently with bulky foods By using the 'Lehmann system' savings of 20–30 per cent of the total meal required from 60 to 200 lb live weight can be obtained with bacon pigs or gilts reared for breeding (Fishwick, 1939, Eyles and Alder, 1955) There are reports of pregnant sows thriving on good grazing only (Hammond 1937) but the limited experimental evidence available (Fishwick, 1939, Ballinger, 1940, Eyles 1959) suggests that supplementary feeding particularly a few weeks before farrowing and after weaning is beneficial It would seem unwise to reduce the amount of meal which can be eaten by a lactating sow with a large litter because sows usually lose body weight when lactating

When fed a full quantity of a balanced ration containing all the recognized nutrients in adequate amounts, non ruminants often thrive better when grazing than when kept indoors (Winter and Schlamb, 1948, Morrison, 1949) They may derive additional benefit from unknown food factors or growth promoting factors (e g grass-juice factor for chick growth Kohler and Graham, 1951) Hormones in

spring herbage (Legg *et al.*, 1950) may stimulate growth of pigs (Gard *et al.*, 1955) and egg production of poultry (Godfrey and Jaap, 1950). Inclusion of lucerne in the diet may enhance the reproductive performance of pigs (Teague, 1955).

EFFECT ON HEALTH

Generally non-ruminants are more healthy when kept out-of-doors on pasture than when kept indoors, provided they are given land free of parasitic infection (Kennard and Chamberlain, 1939; Fishwick, 1935).

Artificial incubation and rearing of chicks to 8 weeks of age indoors has been perfected on a large commercial scale and from the health point of view, there is no case for the use of grazing during this period. Baby pigs from 2 days old have been reared successfully on milk substitutes when housed in heated buildings (Braude, 1954). If litters are suckled naturally, then rearing out-of-doors is beneficial because sow's milk does not supply sufficient iron and piglets obtain it by eating soil (Braude, 1954). In addition sucking litters thrive better, make greater live-weight gains and eat more creep feed when outside on grass than when reared on the sow indoors and given injections of iron (Barber *et al.*, 1955).

Before vitamin requirements were supplied, fertility and hatchability of eggs from hens on grass were better than those from hens kept intensively, but it has been shown that poultry can be bred and reared successfully for several generations under intensive conditions without access to grazing (Anon., 1954). However, in present farming practice, poultry and pigs for breeding and young stock being reared for breeding are normally kept on grassland. It is thought that they are more hardy, take more exercise and have better appetites. Also breeding animals are kept on grassland as a safeguard against errors in the compilation of their diets.

With fattening animals where hardiness and long life is not the aim, the arguments for keeping them on grassland are not strong, especially during the winter when maintenance requirements are increased by cold wet weather and the growth rates are consequently reduced. In sunny warm weather, faster live-weight gains and improved efficiency of food utilization are said to be obtained from fattening pigs full-fed on pasture compared with those full-fed in dry lot (Morrison, 1949), although they use extra energy for grazing. Exposure of laying birds to cold wet weather reduces egg production below that of birds

kept in dry warm conditions (Godfrey and Titus, 1934) On the other hand, laying birds at free range on grassland, feather-peck less than birds kept in flocks indoors However, if kept in folds on grass, outbreaks of cannibalism do occur, so boredom and overcrowding are probably the determining factors (Wilson, 1949) and not the presence of herbage

THE EFFECT ON ANIMAL PRODUCTS

When grass is eaten in quantity the xanthophylls and other pigments cause a dark yellow pigmentation of the skin and legs of poultry and the yolks of eggs (Watson 1939) Dark yellow yolks are preferred by British housewives, but they like the skins of birds for roasting to be white, this is another reason for not feeding grass to broilers With grazing pigs, occasionally the fat of the carcass is tinged yellow and soft fat is formed if excessive herbage intake produces a slow growth rate (Eyles and Alder, 1955)

Occasionally grazing birds produce eggs with green yolks which are caused by the presence of chlorophyll (Worden *et al*, 1955) This occurs more often when birds fed unbalanced diets are grazing luscious herbage in the spring (Davies 1951) but the complete explanation is not yet understood A drawback to keeping laying birds on grassland is the high incidence of dirty eggs due to the mud carried on the feet of the birds This is particularly serious on clay soils in wet winters and when the birds are at a high rate of stocking

CONCLUSIONS ON CLASSES OF NON-RUMINANTS TO BE KEPT ON GRASSLAND

For health reasons it is probably wise to rear and maintain non-ruminant breeding stock on grass all the year round Lactating sows and litters derive benefit from being out-of-doors on grass during the winter and summer However, with our present fund of knowledge it is possible to devise rations and buildings which will maintain both pigs and poultry indoors at a satisfactory level of health and productivity It is possible that in future, economic factors will encourage the spread of such intensive systems of management for non-ruminant breeding stock. Herbage growth is negligible during winter and the nutritive value of autumn-saved growth is very poor for non ruminants For this reason, and others mentioned previously, there is no case for keeping other classes of non-ruminants on grass during the winter There is a good argument for growing pullets laying hens and pigs being

fattened for bacon, to be at grazing in spring and summer, because then they obtain the maximum benefit from herbage and from being out of doors. Chicks from a day old to 8 weeks of age, broilers from hatching to slaughter and weaners being fattened for pork are best kept intensively.

TYPES OF SWARD REQUIRED

Research on pastures suitable for pigs and poultry has been conducted at the Grassland Research Institute, Hurley, England, and conclusions drawn from the results are summarized in the following paragraphs.

Breeding stock require a persistent sward which is hard wearing especially during the winter when recovery is very slow. This type of sward is also needed on the pig or poultry farm of small acreage where pasture can quickly be destroyed by heavy stocking.

On the other hand, growing pullets, laying hens, baconers and in-pig sows need abundant palatable nutritious herbage of low fibre content during the summer. In this type of pasture the aim is to maintain a high percentage of white clovers (wild white, S100 and Ladino), red clovers (late flowering and broad) and lucerne. This is difficult because legumes are so palatable that they are quickly eaten out and the less palatable grasses are encouraged by the high dressings of nitrogen-rich manure (Eyles and Cowlishaw, 1957 and Robinson, 1937; Eyles and Alder, 1955). Wild white clover and S100 are relatively more persistent than Ladino and the red clovers, but the stolons of white clovers are damaged by scratching. The white clovers are valuable for both poultry and pigs, but the larger bulk produced by the red clovers and lucerne is better utilized by pigs.

Because of their leafiness the pasture-type grasses are more palatable than the hay-types. The former produce a closely-knit turf which persists much better than the tufty open sward, produced by the hay-types, which is easily damaged by scratching and rooting (Eyles and Cowlishaw, 1957; Eyles and Alder, 1956). For both poultry and pig pastures S23 perennial ryegrass is the most persistent of all the strains. It is encouraged by frequent cutting and grazing, but because it is so aggressive it dominates the white clovers. Also it is not very palatable and it is susceptible to drought. S24 perennial ryegrass has similar disadvantages but is less persistent. Timothy (S48 and S50) is the most palatable of the grasses (also Ivins and Shaw, 1950) and combines well with white clover. S50 is very resistant to poultry grazing, while

S48 is fairly persistent under pig grazing All strains of cocksfoot produce open swards which do not survive non-ruminant grazing and become too coarse for poultry The meadow fescues are not very palatable to non-ruminants and are not persistent under poultry grazing, but for pigs S53 meadow fescue is next in persistency to the ryegrasses Very persistent species under poultry grazing are S59 red fescue and tall fescue Unfortunately, both form tufty swards and are extremely unpalatable.

Among the herbs, yarrow is very palatable to poultry and makes a remarkably quick recovery in the spring even after complete defoliation in the winter (also Robinson, 1933) Pigs select chicory in preference to grasses

Free-range grazing is better than close-folding because under the latter management the palatable species, particularly the legumes, receive severe defoliation and are unable to recover as quickly as their less palatable competitors When at free-range grazing the animals should be rotated around four areas grazing each for approximately one week. Thus each area has a rest in which the foliage recovers from grazing and the roots replenish food reserves

During the flush of growth excess herbage which cannot be grazed by non-ruminants must be removed by cutting or grazing with cattle and sheep, so that the non-ruminant is presented with young recovery growth and a closely-knit turf is developed. Frequent gang mowing is best for poultry pastures because this encourages white clover and the leafy grasses with prostrate or creeping growth habits (Eyles and Cowlishaw, 1957) Sheep select the legumes and young shoots leaving the mature herbage thus grazing with sheep alone should be for short periods at fairly high stocking rates followed by cutting of the old material and then a rest to allow recovery Mixed grazing of cattle and sheep encourages white clover while growth in excess of non-ruminant requirements is being utilized efficiently by ruminants Lucerne is particularly valuable for pigs in drought periods, but it is killed by frequent cutting or grazing, therefore it should be given a long rest after grazing to allow the roots to accumulate food reserves before the foliage dies back in the autumn (Eyles and Davies, 1958)

Stocking rates should be kept low to allow non-ruminants plenty of herbage from which to select. They can be higher during periods of active growth than during the winter for it is then that most damage is done Dry frosty weather is not so detrimental as a wet winter During the summer, provided there is not a drought, a stocking of

leguminous material must be conserved. When grazing, the animal is able to be selective and hence the material actually eaten has a much higher nutritive value than the herbage on offer, but with cut or processed herbage the animal cannot select, and the value of the material is subsequently less than that of similar herbage which has been grazed *in situ*.

Cut green herbage. The factors which limit the consumption of grazed herbage apply equally to the amount of cut green herbage which can be ingested by non-ruminants. On no account must the cut herbage be mixed with the meal ration, because the animals will not be able to eat sufficient herbage with the mash adhering to it to supply their meal requirements (Temperton and Dudley, 1943). An unrestricted supply of herbage should be provided separately and it must be remembered that wastage tends to be high. If birds eat excessive amounts of herbage, even if it is young clovery material, they develop crop-binding or sour crop. Pigs fed cut green herbage in pens waste a lot of energy in eating and playing with the herbage (Woodman and Evans 1943). In small quantities cut green herbage is valuable as a vitamin A supplement (Eyles and Cowlishaw, 1953) but it is of less value than herbage grazed *in situ* when used to replace large amounts of meal (Woodman and Evans, 1943). The excellent results obtained by Crowther and Heap (1941) when feeding cut grass to fattening pigs appear to be exceptional and not the normal experience.

Dried herbage. The removal of water from herbage eliminates the limiting factor of bulk when feeding large quantities. The fibre content now becomes the controlling influence.

Up to 5 per cent of dried grass can be included in chick rations with advantage, and up to 10 per cent can be included in the rations of laying hens without detrimental effects (Morrison, 1949). However, Cowlishaw and Eyles (1958) have shown that when fed mashes containing 10 or 20 per cent of dried young clover, laying birds ate less mash, produced less eggs, and made poorer live-weight gains, than birds fed mash containing no dried clover, although the levels of crude protein (19.6 per cent) and crude fibre (6.7 per cent) were the same in all rations. This suggests that the dried clover made the rations bulky and less palatable so that the birds were unable to eat enough mash to obtain sufficient nutrients for maximum production (Halnan, 1955).

Up to 30 per cent of the meal ration can be replaced by good-quality dried herbage in the case of fattening pigs (Woodman and Evans, 1948*b*)

and sows (Thompson, 1937). In these cases the dried grass was supplying energy and protein as well as vitamin A.

Increasing the amounts of lucerne meal in the ration is known to depress the growth of chicks and growing pullets (Heywang, 1950) and of growing and fattening pigs (Bohman *et al.*, 1955). By equalizing the fibre and energy levels of the rations, growth depression is not so marked (Hanson *et al.*, 1955; Wilgus and Madsen, 1954). However lucerne does contain a chick-growth inhibiting factor (Lepkovsky *et al.*, 1950), probably a saponin (Heywang and Bird, 1954), the effect of which is counteracted by feeding cholesterol (Peterson, 1950). A factor in lucerne also depressed the growth of swine (Gard *et al.*, 1955). In contrast feeding lucerne meal improved the breeding performance of sows in dry lot (Gard, Terrill and Becker, 1955).

The main value of dried herbage in the rations of non-ruminants has been to supply carotene, which is not so quickly oxidized when mixed into rations as is preformed vitamin A in cod liver oil (Temperton, 1948). If young herbage is dried properly, 5 per cent of freshly dried herbage should supply the vitamin A requirements of all classes of pigs (Davidson, 1952) and poultry (Halnan, 1948). If oxygen can be excluded from the dried grass, loss of carotene during storage can be almost prevented (Booth, 1955).

Hay. Hay is made from more mature herbage than dried grass and consequently is more fibrous and is quite unsuitable for poultry and not generally recommended for pigs. Even best-quality lucerne hay cannot be relied upon to supply their vitamin A requirements (Heywang and Titus, 1932). Chopped leafy legume hay, however, is used occasionally in the United States for pigs, particularly pregnant sows (Morrison, 1949). The valuable leaf is easily lost in curing, but if made well in bright sun not only does it contain carotene but also appreciable quantities of irradiated ergosterol. Because it is more fibrous, hay can replace much less meal in the diet of pigs than dried grass.

Silage. It is difficult to make good silage from young leguminous herbage and also the process destroys some of the nutrients and vitamins. Offered good silage without stint, birds fed a full amount of a nutritionally complete meal had a slightly better egg production than those without silage, but some of the eggs were tainted by the silage smell (Eyles and Cowlishaw, 1956). Hens eating silage may produce eggs with dark-coloured or greenish yolks (Gish *et al.*, 1940). The birds cannot consume large amounts of silage, therefore very little

saving in quantity of meal can be made, and they may not eat enough to supply their requirements for vitamin A (Olsson *et al.*, 1951) or for riboflavin (Clark *et al.*, 1949).

Although silage is of limited use to poultry pigs, especially in-pig sows (Terrill *et al.*, 1953), will eat appreciable amounts of it provided that its fibre content is sufficiently low.

Herbage leaf-protein extracts. In an attempt to make a protein concentrate from pasture plants, juice was squeezed out of green macerated herbage, the precipitate formed by heating this juice was filtered off, dried and ground (Pirie, 1952, Tilley *et al.*, 1954). The resultant dark green powder contained approximately 40 per cent of crude protein, 10 per cent of soluble ash and below 2 per cent of fibre. Thus to non-ruminants, fibre is not a limiting factor to the increased consumption of these extracts.

The complete replacement of fish meal by 'leaf protein' in practical rations for chicks (Hughes and Eyles, 1953), laying hens (Cowlishaw and Eyles 1956), suckling piglets, weaners and lactating sows (Eyles, Tilley and Raymond, 1956) resulted in poor production even when quantities of minerals, vitamins and animal protein factors equal to those in fish meal were included in the 'leaf protein' ration. For growth in pullets 'leaf protein' satisfactorily replaced fish meal. If included at high levels (28 per cent in chick rations, 19 per cent in weaner rations) these crude extracts were definitely harmful, causing excessive pigmentation in chicks and scouring in pigs.

Extensive chick trials using the 'Gross Protein Value' technique have been conducted (Cowlishaw *et al.*, 1956) to discover why these extracts had a poorer feeding value than was predicted from amino-acid analysis (Ellinger, 1954). It has been confirmed that extracts obtained from lucerne contain a growth-inhibiting factor, probably a saponin, which is counteracted by the addition of 0.3 per cent of cholesterol to the ration (Cowlishaw *et al.*, 1954). Water-washing of the extracts reduces the growth-inhibiting action. This factor is not present in extracts of grasses or white clover so far tested. The addition of lysine to rations containing 'leaf protein' improves chick growth which suggests either that these extracts are deficient in lysine or that this amino-acid is unavailable.

When fed to rats the biological value of the protein in these extracts was higher than that in groundnut meal (Ellinger, 1954), but it had a lower digestibility. A colourless cytoplasmic fraction had a higher digestibility than the crude extracts (Davies *et al.*, 1952). When fed

to chicks, high 'Gross Protein Values' were obtained with a cytoplasmic fraction suggesting that the chloroplastic fraction present in crude extracts was of poor nutritive value (Cowlishaw *et al.*, 1956). Faeces of both poultry and pigs fed on rations containing crude extracts are dark green, showing that the plant pigments remain undigested. Removal of these pigments and chlorophyll by solvent extraction using alcohol and acetone did not improve appreciably the 'Gross Protein Value'. The pH at which precipitation is done and the methods of drying the resultant curd had no effect on the feeding value of the final products. Allowing the wet curd to ferment produces a material of very poor feeding value.

Present knowledge indicates, therefore, that crude leaf-protein extracts can only be used in practical rations as another vegetable protein concentrate to replace part but not all of the animal protein in the rations of non-ruminants.

INTEGRATION OF POULTRY AND PIGS INTO GRASSLAND FARMING

On the mixed farm of a moderate or large acreage there is a good opportunity to take full advantage of grassland for saving other feeding stuffs and for maintaining the health of non-ruminants. Pigs and poultry can be given free-range rotational grazing at a low rate of stocking and can be moved frequently to uncontaminated land and need not be returned to the same area for years. While grazing, they distribute their manure without loss of plant nutrients direct to the land, thus eliminating the labour of carting manure, and at the same time increasing herbage production which can be efficiently utilized by sheep and cattle. This grazing helps to maintain the swards in a young stage of growth with plenty of clover for non-ruminant grazing. A useful three-year ley for poultry is one containing S50 timothy, yarrow and white clover, and for pig grazing a suitable three-year ley would consist of white clovers, chicory and S48 timothy. Both of these swards would also be valuable for ruminants. Swards of perennial ryegrass (S23 or S24) or of meadow fescue (S53 or S215) with white clovers, which are useful as three-year leys for sheep and cattle, can also be utilized for non-ruminants. Lucerne/meadow fescue stands and one-year leys of red or white clovers can be cut for conservation or grazed occasionally by ruminants, as well as being valuable grazing for poultry and pigs. The scratching and manuring of poultry

improves old pastures and pigs are useful for reclamation of derelict grassland and scrub.

Elaborate permanent housing is not required for non-ruminants kept on grassland, but on the other hand labour costs for feeding and moving of houses are often increased. Labour can be reduced by feeding pelleted rations direct on to the sward and this also prevents the losses incurred when meals are fed in the field. Self-feed hoppers are labour-saving but the animals eat excessively and no saving of concentrates can be made, they must be encouraged to graze by keeping the hoppers closed during the morning. Paraffin, which must generally be used in the fields, is not so convenient or so safe as electricity for lighting (egg production) and heating (brooding of chicks and piglets). The supply of water, particularly in frosty weather, is a problem. Permanent fencing is expensive although this can be reduced by using electric fencing for pigs, and sheep fencing for poultry if the feathers on one wing are kept clipped to prevent flight.

During summer less labour is used if non-ruminants are allowed to graze herbage *in situ* as compared with green-soiling it or conserving it and feeding the product indoors In addition, reciprocating mowers, and most loaders used for hay and silage making, are unable to deal with the very short material which is required The herbage must be cut by a machine fitted with helical-blade mowers and then the herbage sucked into a trailer Large quantities of water have to be handled and the cost of drying succulent herbage is high The production of dried grass used to be justified as it was the most reliable source of vitamin A for non-ruminants kept indoors, but with the advent of cheap synthetic powders containing stabilized vitamin A, this is no longer the case.

A distinct problem occurs on the specialized poultry and pig farms of small acreage. Here rotational grazing must be practised to allow the sward to recover and to keep it free from disease. To reduce the stocking rates, chicks, growing pullets, laying hens and fattening pigs must be kept indoors and only breeding stock allowed to graze on hard-wearing swards of S23 perennial ryegrass and wild white clover. Alternative seeds mixtures would be for poultry S50 timothy, yarrow and wild white clover and for pigs S53 meadow fescue plus wild white clover. Permanent pastures with matted turf are resistant to poultry and pigs and are often improved by the scratching and manuring. The last year of a ley before ploughing is perhaps the best sward to use for non-ruminant grazing because in this case it does not matter if

extensive rooting and scratching occurs. Purchased dried grass, if cheap relative to other feeding stuffs, could be used in large quantities in the rations of bacon pigs and in small quantities to supply vitamin A in all rations fed to stock kept indoors.

TURKEYS

Before the introduction of efficient drugs for the prevention and cure of blackhead, coccidiosis, bacillary white diarrhoea and internal parasites, intensive methods for brooding, rearing and fattening turkeys were developed because of the high mortality caused by these diseases when birds were run on contaminated land. Probably it is best to rear away from the soil until ten weeks of age and then offer grazing on clean land. Turkeys are natural grazers, and Margolf (1952) reported that they select Ladino white clover in preference to grasses to such an extent that it was killed out after only one year.

Turkey poults older than ten weeks can thrive on high-fibre rations (15 per cent crude fibre). To obtain their energy requirements, larger amounts are eaten than with low-fibre rations (Dymsza *et al.*, 1955). Thirty-five per cent of good-quality alfalfa meal has been fed to growing poults without adverse effects on growth or feed conversion (Alder, 1946), and pelleting of these high-fibre rations enables the birds to increase consumption and so obtain sufficient energy (Slinger *et al.*, 1949). Probably good grazing can be used to save appreciable quantities of meal. When grazing, herbage supplies their requirements for vitamin A, and the protein level of the mash can be lowered to 10 per cent of crude protein without adverse effects on growth. Cereals and minerals plus good clover pasture produced satisfactory growth and food conversion (Margolf, 1952). Breeding turkeys should be given free range grazing on young pasture growing on clean land, because ingestion of herbage improves the hatchability of eggs (Slinger *et al.*, 1954).

GEESE

During the first six weeks of life goslings must be fed mash and grain, but after that age they make good growth solely by grazing young summer herbage (Wright and Dudley, 1942). However, during winter when grass is fibrous and of low nutritive value mash must be fed (Howes, 1943). Gosling broilers reared in confinement up to

14 weeks of age made better growth and were of superior quality compared with those grazing pasture, but the latter both consumed less mash, and made more efficient use of it (Snyder *et al*, 1955) Grazing should be supplemented with grain and possibly mash during the laying period

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CHAPTER THIRTEEN

Bloat

A T JOHNS

Types of bloat—Animal factors gas production saliva, microbiology and slime, eructation—Plant factors saponins, protein, anti-foaming agents, other compounds—Cause of bloat—Cause of death—Prevention and treatment

The adaptation of the ruminant stomach to provide a large sac for the microbial fermentation of ingested plant material results in these animals having to eliminate a large volume of gas by belching Normally they have no difficulty in doing this, but in a condition known as bloat (or tympanites or hoven) failure to eructate can cause a rapid distension of the rumen, and this may lead to death if not relieved. Most species of ruminant can be affected but dairy cows appear to be the most susceptible

Bloat occurs in all parts of the world where the grazing of legumes is practised In the United States the feeding of concentrate rations used for 'finishing off' cattle can give rise to a condition known as 'feed lot' bloat It has been claimed that the incidence of pasture bloat has been steadily increasing in recent years, concurrently with the introduction of more vigorous clover strains The validity of this claim is difficult to substantiate or refute, but it is certain that bloat is not a recent phenomenon A description of the ailment written in A D 60 is available (cited by Tribe, 1947), and Beddows (1952) has collected together many historical extracts on the incidence of bloat from writings of the early eighteenth century Mortimer in 1716 (quoted by Beddows 1952) wrote of clover-grass

Great care must be taken of cattle that are first put into it, lest it burst them. To prevent which, some gave them straw with it and some stint them as

to quantity but the best way is only to turn them into it the first day about noon, when the dew is off, and in a dry day, for about half an hour, the next day for an hour, the third day for two, and then for three or four days put them in as soon as the dew is off the ground, and let them stay in till four or five in the afternoon, and after that there will be no danger especially if 'tis not too wet weather. If 'tis, be the longer before you let them stay in all night. However 'tis better for any other cattle than Milch Cows. But some sow Trefoil or Ray-grass with their clover; which very much prevents it doing injury to cattle; and as 'tis a grass that grows very upright, it shoots through the branches of the spreading clover, and makes the crop much better.

These views have been largely held by farmers up to the present day. They have not been fully refuted or proved largely on account of the sporadic nature of the ailment and the difficulty in producing it under experimental conditions.

In a country such as New Zealand where animals are at pasture all the year round, and where the farmer is dependent on the clovers in his sward for his source of nitrogen, bloat is the major scourge of the dairy industry. In the two dairying seasons 1953–5 the losses due to deaths alone amounted to £500,000. The number of cows dying from bloat is by no means a measure of the full economic loss. It takes no account of the loss of milk production both from animals which die and those that recover. Besides the loss of production during bloating, lactation after recovery is often curtailed or even terminated. The physical and mental strain on a farmer and his family has to be seen to be appreciated. Bloat may prevent a farmer carrying out his normal duties, upset his grazing rotation, and force him to use up reserves of hay and silage. It may also make the farmer reluctant to use clovers in his seeds mixture, which must lead to a reduction of fertility.

Bloat is a confusing entity, much more complex than has been generally realized, in which both plant and animal factors play a part. Interest in the problem has increased markedly over the past few years and the major part of the more recent work has been covered in reviews by Dougherty (1953), Cole *et al.* (1956), Johns (1956) and (1958), Cole and Boda (1960).

TYPES OF BLOAT

Bloat has in the past been frequently classified as either 'foaming' or 'free-gas' type. The difficulty lies in determining whether foaming

is present or absent It is believed by the author that many people have considered bloat to be of the non-foaming type if free gas is present in the rumen dorsal sac However, even in foaming bloat there always appears to be a gas pocket present which may vary in size according to the stability of the foam and progression of the condition (see also Boda *et al*, 1956) In studies carried out at this laboratory (Plant Chemistry Division, D S I R, Palmerston North, N Z) no bloat has been encountered which is not prevented or relieved by anti-foaming agents Hence it would appear to be wise to avoid the classification of bloat on the presence or absence of foaming as a criterion

Cole *et al* (1956) have suggested that bloat should be divided into three types, chronic, sub-acute and acute, and points out that 'chronic' means a condition that is lingering, one which is inveterate, of long continuance or progressing slowly, as distinct from an acute disease which speedily terminates Chronic bloat, which will not be the subject of this chapter, can be due to a wide variety of causes, such as an obstruction of the oesophagus, peritonitis, enlarged mediastinal glands, paralysis of the rumen-reticular musculature, anaphylactic shock, hypocalcaemia, or dwarfism

Pasture bloat is definitely not chronic, being characterized by a rapidity of onset and speedy recovery, hence it may be termed acute Sub-acute bloat, as a division of the acute type, is used to describe the milder state which has not progressed to the stage where marked discomfort, as evidenced by frequent urination, defaecation, bellowing and staggering, is manifest. Acute bloat in which these signs are manifest may only be a later stage of the sub-acute state making such a division into two stages unwarranted On the other hand there may well be two stages in the development of the condition, i e

(1) Foaming of the rumen contents may cause a retention of gas in the froth

(2) As distension progresses a critical pressure may be reached which interferes with the eructation reflex itself and causes the more distressing form of the ailment

Further research work is necessary to elucidate these points

'Feed-lot' bloat, which is experienced chiefly in the U S A on a ration of grain and hay, appears to be due to foaming of the rumen contents, and can consist of sub-acute bloat more or less chronic in nature (Lindahl *et al*, 1957)

The contribution that possible animal and plant factors make to the state of the bloated animal are discussed separately below.

ANIMAL FACTORS

It is well known that certain animals in a herd of cattle are more susceptible to bloat than others. It has been widely held that it is the high producers and greedy eaters that are the bloat-prone animals. However, Johns (1954) showed that the tendency to bloat bore no relationship to the rate of food intake nor to the amount eaten. In fact bloated animals had on the average a lower intake than the non-bloated, which was also observed by Hancock (1954) and Lindahl *et al.* (1957). It appears that the predisposition to bloat is an inherited characteristic (Knapp *et al.*, 1943; Hancock, 1953; Johns, 1954). However, the difference between susceptible and non-susceptible animals is not absolute but a matter of degree. When bloating conditions are severe enough the whole herd can be affected. Moreover the susceptibility of particular animals does not necessarily remain constant. During a feeding period of several months it has been found at this laboratory that some pairs of identical twins may be prone to bloat while others are not. At some stage non-susceptible twins may become susceptible to bloat and *vice versa*, the members of the twin pair behaving similarly. Hence the basis for the hereditary differences between animals would appear to be due to an effect on the state of the rumen or condition of the animal rather than to any anatomical difference (Johns, 1958; Mendel *et al.*, 1960).

There are a number of factors which can influence the state of the animal which will be considered below.

GAS PRODUCTION IN THE RUMEN

The most obvious conclusion that one reaches in observing a bloated animal is that the beast is producing more gas in its rumen than it can eliminate by belching. There appear to be two possible reasons for this: (1) either there is excessive gas production in the bloat-prone animal, or (2) the produced gas is trapped and is not in a form that can be eliminated by eructation.

(1) The theory of excessive gas production was widely accepted until comparatively recently (Quin, 1943). However, the finding that ruminal gas production can be as high on non-bloating as on bloating rations (Cole *et al.*, 1942) and the fact that if no other

complicating factor is present the animal has no difficulty in getting rid of all the gas that could be formed in its rumen (Quin, 1943, Cole *et al*, 1945), led to the belief that rate of gas production *per se* was not of major importance in the aetiology of bloat The present author has argued that as the amount of gas formed by fermentation in the rumen is roughly proportional to the amount of herbage ingested, and as it was found by Johns (1954) that the dry-matter intake of severely bloated animals was on the average less than that of milder cases, the bloated animals would be expected to be producing less gas by fermentation than the non-bloaters However, this reasoning did not take into account the fact that animals on the same diet can have rumen contents with differing microbial populations (Oxford, 1955, Moir, R. J, personal communication) Hungate, *et al* (1955) found indications by an *in vitro* technique that more gas was produced, after feeding from the ingesta of bloating cows than from non-bloating animals The present author, using an *in vitro* technique, found that the rumen contents obtained from twin animals on the same feed can ferment the similar added substrates at markedly different rates It seems likely that the greater the *rate* of gas production by a particular microbial population the more severe will be the bloat condition if there is an interference with the process of gas elimination.

(2) Primarily as a result of the studies in South Africa (Quin, 1943, Clark, 1948, 1950*a*, Weiss, 1953*a*) the fact that frothy bloat does occur is widely accepted Whether it is the only type of pasture bloat is an open question In several years' work at our laboratory we have not experienced bloat which will not respond to antifoaming agents Hence it appears that at least a major cause of the ailment is the trapping of gas in a foam There always appears to be some free gas present The stability of the foam and rate of gas production will no doubt determine how much is retained within the ingesta and how much escapes to form a free gas pocket

Kleiber (see Cole *et al*, 1956) has dealt fully with the sources of rumen gases which are principally carbon dioxide (CO_2) and methane These are produced in large quantities by the anaerobic fermentation of ingested food concurrently with the formation of large amounts of the lower volatile fatty acids The continuous secretion of saliva (60 litres per day for a cow Colin, 1886) high in bicarbonate also provides a not inconsiderable source of CO_2 in the rumen Kleiber has calculated that each litre of saliva at pH 8 2 entering the rumen in which the contents are at pH 5 7 releases approximately 2 litres of CO_2

Hence if the figure of 60 litres of saliva per day is accepted (see below) the total CO_2 from saliva would be approximately 120 litres per day at a rumen pH of 5·7.

From the point of view of bloat it is probably the rate of release of gas within the first hour that is important. Animals in our laboratory frequently show a pH change from 7·4 to 6·3 or lower within the first hour after the start of feeding on red clover and may go as low as pH 5·6 in the next hour. Hence a fermentation which is rapid will, besides contributing directly by the gas formed, also release more CO_2 from the rumen contents by a rapid increase in acidity.

SALIVA

As mentioned above mixed bovine saliva is high in bicarbonate. Reid and Huffman (1949) also pointed out that it must contain a potent surface active agent as its surface tension is in the range of 45–9 dynes per cm. when compared with water, the value of which is given as 73 dynes per cm. It would consequently be expected to be a good foaming agent. Mangan (1959) has found that the mucoprotein of saliva aspirated from under the tongue will form a very stable foam.

Clark and Weiss (1952*a*) demonstrated the existence of a salivary reflex initiated by stimulation of the epithelium of the forestomachs. Weiss (1953*a*) believed that bloat in sheep on succulent feed was caused by frothing of the thick viscous rumen ingesta insufficiently diluted with saliva to allow the gas bubbles to rise to the surface. When mature stalky lucerne was given, the increased saliva flow caused the rumen ingesta to revert to a watery consistency. Hence Weiss suggested that bloat was due not to a lack of stimulation of belching (see below) in the absence of coarse fibre, but to a lack of stimulation of salivary secretion. In support of the theory that the dilution effect is important Mendel (1960) has shown that 'bloaters' have a lowered salivary rate both during rest and during the ingestion of feed.

There is no doubt that the amount of saliva secreted is related to the condition of the food as Balch (1958) has shown that for 10 lb. of food, a cow secretes 45–55 lb. of saliva when fed hay, 12–15 lb. with ground concentrates and 7·5–10 lb. with grass. However, it is difficult to reconcile Weiss' theory of lack of salivary secretion with the fact that bloat has been produced on hay (Johns, 1954) and by a number of workers by drenching with legume juice.

In considering the role of saliva, neither by previous workers nor in the discussion above has account been taken of the fact that there are at

least four components of mixed saliva with very different properties (Phillipson and Mangan, 1959)

(1) The parotid secretion is continuous and watery, high in bicarbonate (0 1M) and buffering power The parotid flow is reflexly increased by feeding
(2) The submaxillary glands secrete only during the taking of food This saliva is viscous, much lower in bicarbonate (01M) and buffering power than the parotid, and contains a considerable amount of muco-protein with strong foaming properties (Mangan, 1959)
(3) A third salivary secretion, the sublingual, appears to combine the properties of the two mentioned above, being high in protein and in bicarbonate
(4) The residual secretions from the buccal glands make a further contribution of unknown quantity

Theoretically a large secretion of saliva could, according to its composition, increase bloat severity by adding to the CO_2 evolved and by assisting in foam formation

Inflation of the rumen of anaesthetized sheep and calves increases salivary flow (Phillipson and Reid, 1958) The results from sheep are more variable than those from calves Parotid secretion is augmented at pressures varying from 10 to 20 mm Hg, the increase may be as much as 8 times the resting value A fivefold increase in the submaxillary secretion was obtained in one calf Inhibition of the augmented flow usually occurs when the pressure is further increased Variability from animal to animal was found in the pressure needed to stimulate salivation and the pressure needed to produce subsequent inhibition This effect appears to depend on whether or not gas or food enters the thoracic part of the oesophagus Distension of the rumen alone, if the oesophagus is tied at the cardia, is inhibitory to salivation but distension of the thoracic oesophagus stimulates profuse salivation (Kay and Phillipson, 1959)

It may well be with an animal that has an increased saliva flow in response to rumen pressure that when mildly bloated, the extra CO_2 contributed from saliva could tip the balance in determining whether the bloat will be severe or not For it was found in a 5-months-old calf that the amount of CO_2 necessary to raise the pressure 10 mm Hg was much less at high than at low pressures as shown below

Pressure increase in rumen in mm. Hg.	Volume of CO_2 required in litres
2·5–10	20·8
10–20	4·8
20–30	2·7
30–40	2·2

Lindahl *et al.* (1957) rated animals for degree of bloat and took direct pressure readings from fistulated animals. According to their scale a pressure reading of 10–15 mm. represented slight bloat; 25–35 mm., moderate; 45+ mm., severe bloat. Hence at a pressure of 20 mm. (slight to moderate bloat) where a markedly increased saliva flow can occur in some animals, a source of gas additional to that being formed by bacterial fermentation could be serious.

The role of saliva in bloat, particularly with regard to animal individuality and the development of the fatal condition, appears to merit further investigation.

MICROBIOLOGICAL FACTORS AND SLIME PRODUCTION

It was pointed out in the section on gas production that it is possible for animals on the same diet to have differing microbial populations in their rumens. However, as yet it has not been possible to demonstrate convincingly a difference in the types or numbers of organisms between bloating and non-bloating animals that can be regarded as being responsible for the production of bloat. Mah and Hungate (1960) reported that the ingesta of bloating animals contained greater numbers of protozoa belonging to the genus *Ophryoscolex* than the ingesta of non-bloating animals. However, the numbers reported as being present were low. Bryant *et al.* (1960) found in animals pastured on ladino clover, that the anaerobic bacterial counts were high, the proportions of cellulolytic bacteria were very low, the proportions of the genus *Butyrivibrio* were high and those of the genus *Lachnospira* were unusually high. There were, however, no significant quantitative or qualitative differences between the rumen micro-organisms cultured from bloating and non-bloating animals.

An hypothesis involving a change in the nature of the ingesta to explain at least in part the cause of frothy bloat has been advanced by Hungate *et al.* (1955) for legume bloat and by Jacobson and Lindahl

(1955) for 'feed lot' bloat Hungate *et al* (1955) in considering the differences in properties of the rumen ingesta from 'bloaters' and 'non-bloaters' on the same food, thought it questionable whether these could be explained by differences in the rate of fermentation of plant material or of released foaming agents He advanced the idea that the rumen contents of regular 'bloaters' contained a higher proportion of slime-producing micro-organisms This microbial slime could contribute to the formation of a stable foam. A similar hypothesis was put forward by Jacobson and Lindahl (1955) for 'feed lot' bloat, where the adaptation to the bloating condition may take many weeks on the same food This adaptation was shown to be accompanied by a gradual increase in the number of slime-producing organisms present in the rumen (Jacobson *et al*, 1957)

Gutierrez *et al* (1959) suggested that the increased numbers of slime-producing *Streptococcus bovis* and *Peptostreptococcus elsdenii* producing a filamentous mat in animals bloated on the 'feed lot' type of ration might be involved in the production of a stable foam. Bailey (1959) found the concentration of polysaccharides in cell-free rumen liquor from cows feeding on red clover to be low and similar in bloating and non-bloating animals The concentration of capsular polysaccharides in the centrifuged solids showed no correlation with bloating Dextran might have been expected to be present, since the level of sucrose in the herbage, 2 5–3 5 per cent dry weight (Bailey, 1958) and the presence of *Streptococcus bovis* in the rumen favoured its formation (Bailey and Oxford, 1958) It was not found, however, though it may have occurred transiently before being broken down by dextranase-secreting strains of *Lactobacillus bifidus* found to be present (Bailey and Clarke, 1959)

Though it appears that bacterial polysaccharides have not been proven to be responsible for foam formation in pasture bloat, the fact remains that there is a difference in the physical properties of rumen contents of bloating and non-bloating animals The responsible agent or agents have yet to be found.

ERUCTATION MECHANISM

The eructation of gas produced in the rumen from fermentation and from the bicarbonate of saliva is of necessity a complex act on account of the anatomy of the organs concerned The gas collects as a pocket in the dorsal rumen at a point rather higher than the cardia, the entrance to the oesophagus The cardia is in fact normally below

the level of ingesta. Eructation has therefore to be a co-ordinated process involving activity of the reticulum, rumen and oesophagus. This results in the clearing of the cardia of ingesta, the bringing of the gas bubble forwards and downwards, and the opening of the cardia at the appropriate time to allow the passage of gas into the oesophagus. The sequence of events in eructation is covered in detail by Dr A. T. Phillipson in Chapter 7.

In the past it was considered that the belching reflex was similar to the regurgitation reflex and the stimulus was the scratching of the stomach wall by roughage (Cole *et al.*, 1942). However, it is clear from more recent work that two very different reflexes are involved. The stimulus initiating the eructation reflex is now generally believed to be stretching of the stomach wall (Weiss, 1953*b*; Iggo, 1955, 1956; Williams, 1955). Weiss (1953*b*) found that during insufflation experiments under a given set of conditions eructation efficiency was proportional to intra-ruminal pressure. Johns (1954) found that with increasing pressure during the onset of bloat on clover, when according to the theory of Cole *et al.* (1942) there is insufficient roughage, frequency of eructation increased rather than decreased.

Dougherty and his co-workers (1955), who were the first to demonstrate the action of three oesophageal sphincters, consider that there are receptors involved which can distinguish between gas pressure, which stimulates the opening of the cranial oesophageal sphincter, and fluid or foam pressure which does not. This offers an explanation why foam is not belched out except *in extremis*, as it appears to elicit the same response as liquid. In the early stages of legume bloat it does not seem that the eructation reflex is impaired; if anything, the belching rate is increased (Johns, 1954; Hancock, 1954). The higher pressures of acute bloat may inhibit eructation.

PSYCHOLOGICAL CONDITION

Weiss (1953*b*) pointed out that the psychological condition of the animal may play an important part in the pathogenesis of bloat. He saw bloat occurring in a herd coincidental with the change-over from hand to machine milking. Reid (personal communication) witnessed cases where a herd of cows, which had experienced bloat in a particular field, bloated while being driven to that area. It appears that nervousness may occasionally be a factor in proneness to bloat.

PLANT FACTORS

The chemical make-up of plants in bloat production is obviously important Chemical factors will affect the rate of gas production from fermented plant material The effect of the physical state of the fodder has already been discussed

There have been a number of theories concerning bloat, where it was believed that toxic factors in the plant material, or produced from plant material by bacterial fermentation, inhibited rumen movement or the eructation mechanism or caused systemic poisoning The factors incriminated at various times have been the cyanogenetic glucosides of white clover, saponins, histamine, anticholine esterases, smooth-muscle inhibiting flavones, nitrates, ammonia, ammonium carbonate, hydrogen sulphide, alkalinity and lack of fibre However, Wester (1935) noted that there is hypermotility in the early stages of acute bloat rather than inhibition of movement Weiss (1953*b*), Johns (1954) and Lindahl *et al* (1957) have confirmed that in animals examined with bloat, the rumen was in active movement It was difficult to determine whether the strength of the movements was in any way reduced Recent work at this laboratory would indicate that there is no reduction in the strength of rumen movements at least in mild bloat

The results of a number of workers show clearly that the primary cause of the majority of cases of bloat is not an inhibition of rumen motility *per se* but rather the retention of a greater part of gas within the rumen ingesta

Acute bloat has been produced by the oral or intraruminal administration of pressed juice from legumes and attempts have been made to correlate the foaming capacity of legume juice with its bloating potential For instance, Ferguson and Terry (1955) found that the frothing capacity of juice from fresh lucerne expressed from a triple roller mill gave a fair indication of its bloating potential However, Mangan and Johns (1957) found no significant differences between the foaming properties of macerates prepared from herbage of widely differing bloat-inducing potencies

As outlined by Johns (1956) the type of foam present in the rumen is of the surface viscous type, of which protein and saponin foams are typical examples These are incompatible with non-viscous foams formed by soaps and detergents

McCandlish (1937) was the first to suggest that plant saponins were

a contributing factor in bloat, while Johns (1954) has suggested that proteins could be important from the point of view of their foaming properties. The following sections consider each in turn.

SAPONINS

Jacobson (1919) fed so-called 'saponin' to an animal in an unsuccessful attempt to produce bloat. Lindahl *et al.* (1954) appear to be the first to have produced bloat by dosing a saponin isolated from a pasture legume. In this case the mixed saponins dosed to sheep were isolated from lucerne by workers at the Western Regional Research Laboratory, United States Department of Agriculture, California, who have carried out extensive work on these plant constituents. It appears doubtful whether the condition resulting from the dosing of saponins is similar to that obtained during legume bloat. In cases where death occurred *post mortem* examination has indicated that death was associated with an intense submucocosal and subserosal haemorrhagic condition of the gastro-intestinal tract. Such lesions are not obvious in deaths from pasture bloat.

The work of McClay and Thompson (see Cole *et al.*, 1956) in analysing various forages for saponin content does indicate that there is possibly a correlation between the saponin content of a species and its ability to produce bloat. By contrast Barrentine (1960) found no relationship between the saponin content and the bloat potential of ladino clover, crimson clover, hop clover, alfalfa or lespedeza. One of the present limitations in testing the role of saponins is that there is no simple method available of measuring the level of saponin in the herbage in order to determine its day-to-day correlations with bloat.

Mangan (1957) has determined the pH optima for maximum foam stability for several compounds including a saponin fraction from red clover and a sample of lucerne saponin kindly supplied by Dr C. R. Thompson of the Western Regional Laboratory. For both of these, the optimum is in the region of pH 4·5–5. There was very little foam stability at pH 6 which is the pH optimum for maximum foam stability of rumen contents from bloating cows (Mangan, 1957). On this evidence it would not appear likely that saponin plays much part in producing foam in the rumen. In the saponin drenching of Lindahl *et al.* (1954) it was considered that the distension was caused by the presence of free-gas rather than froth. When the foaming capacity of legume extracts was compared with that of purified lucerne saponin

(Mangan, 1957) the results showed that we would have to postulate an absurdly high plant saponin content to account for the foaming properties of the extracts However, as the saponin was prepared from dried lucerne it may be that the saponins used had lost foaming capacity in the isolation procedure (see Mangan and Johns, 1957) Obviously more work is needed on the saponins before their role is elucidated

PROTEIN

It was postulated by Johns (1954) that protein or its degradation products could play a part in foam production in bloat Ferguson and Terry (1955) have pointed out that bloat can develop in 15-20 min after the commencement of grazing and the bloat-provoking principle must therefore diffuse out of the plant material rapidly These authors go on to say that it is doubtful if much of the ingested protein would be released from unchewed tissues within this time However, enough does escape rapidly into the rumen to form a stable foam (Lyttleton, Mangan and Reid, unpublished results) In results obtained in this laboratory (Mangan *et al*, 1959) it has been found that when the degradation of protein in the rumen is inhibited by dosing with penicillin, the soluble protein nitrogen can rise from 12 mg to 38 mg of protein N per 100 ml in one hour Even in an untreated animal feeding on red clover the rise was from 3 9 mg N before feeding to 19 3 mg N per 100 ml in one hour after the commencement of eating Mangan (1959) has also found that in the presence of salt the red clover cytoplasmic protein at a concentration of 20 mg protein N per 100 ml formed a very stable foam with a maximum stability at pH 6 0 and that the foaming potential of rumen liquor parallels the changes in concentration of cytoplasmic protein.

The occurrence of bloat on young spring grass high in protein is not infrequent in the United Kingdom and has been produced experimentally in New Zealand

It appears that the conditions in the rumen and protein concentration after feeding are such that plant protein could play a part in the production of a stable foam

ANTI-FOAMING AGENTS

In a study of the action of penicillin in preventing bloat it was found that the antibiotic had a profound effect on the foaming proper-

ties of rumen contents (Mangan *et al.*, 1959). The foam expansions and foam stabilities of the crude rumen liquor from a penicillin-treated cow were found to be very low compared with those of the control animal. This was in spite of the fact that the treated animal's rumen liquor had a very high soluble-protein content. By contrast the *centrifuged* rumen contents from the treated cow showed a very high foam strength. This very great increase in strength of the foam produced from the centrifuged rumen liquor of the penicillin-treated animal (in agreement with the high soluble-protein content) as compared with the strength of foam from the crude liquor, indicated that a strong anti-foaming agent was present and was removable by centrifuging. It had been postulated (Mangan, 1957) that the plant chloroplasts, with their envelope of lipid, have anti-foaming properties and that the results obtained in centrifuging rumen contents is due to their removal from the liquor. If the foaming properties of the rumen liquor had been due to any capsulated slime-producing bacteria as discussed above, centrifuging should presumably have reduced the foaming properties of the rumen liquor. It appears possible that the degree of foaminess of rumen ingesta is in part at least determined by the particular ratio of foaming to anti-foaming agents present.

OTHER CHEMICAL COMPOUNDS

Conrad *et al.* (1958) found that washed lucerne fibre produced *in vitro* on an average three times the amount of gas obtained with an equal weight of lucerne juice. They claim that the plant substances responsible for the initial rapid gas production obtained with green lucerne are closely associated with the fibre fraction and are removed by extraction with hot water. From their experimental results they believe that the stable foam found in pasture bloat is due to the combined effects of the physical structure of lucerne fibre, pectic substances of lucerne, galacturonic acid obtained by the hydrolysis of pectic substances and reducing sugars. A possible weakness of the *in vitro* work of Conrad *et al.* is that the rumen ingesta used was from animals fed on grain and hay. This diet may well have produced a rumen microbial population more favourably disposed to the digestion of fibre and starch rather than the soluble constituents of lucerne juice. In contrast to the opinion of Quin (1943) and of Rosen *et al.* (1956), studies by Mangan and Johns (1957) failed to show a correlation between either soluble sugars or organic acids and bloat.

GENERAL REMARKS

The correlation between the production of bloat-prone pastures and weather conditions is claimed to be very marked in some districts However, the theories as to the type of weather involved are many and varied In the controlled experiments of Johns (1954) no particular condition could be consistently blamed for the production of bloaty red clover A considerable amount of work since that time has not altered this conclusion Troughton (1955) in grazing trials on white clover found no correlation between maximum and minimum temperatures, rainfall, sunshine or humidity, and the quantity of bloat produced per day

Both fertilizer treatment and soil-mineral deficiency have been claimed to induce bloat It is difficult to determine, however, whether the treatment has influenced the chemical composition of the plant, or whether, by making conditions more suitable for growth, it has altered the balance of species in the pasture association

It appears likely that the climatic and soil factors necessary for the development of bloating potential in clover will be determined only when the substances present in plants responsible for bloat production can be estimated

CONCLUSIONS ON THE CAUSE OF BLOAT

The evidence obtained from research work on pasture bloat as outlined above, particularly over the last few years, indicates that the primary cause of legume bloat is a retention of gas in the frothy rumen ingesta Moreover, most workers are agreed that the problem is a complex one in which both plant and animal factors are involved. The term 'animal factors' is intended to include the rumen micro-organisms

Many of the difficulties encountered in work to date in attempts to unravel the complex interactions that result in the state known as bloat are probably due to the failure to recognize the importance of the condition of both the plant and the animal It is coming to be recognized that animals on the same diet need not necessarily have the same rumen flora and fauna and that the animal itself can in some way influence to some extent the numbers of organisms that proliferate in its intestines

For bloat to occur we believe that the rumen must be in a suitable condition. There must be a vigorous fermentation to produce gas,

and fatty acids, which lower the pH of the rumen contents, with a consequent additional gas production from the bicarbonate of saliva. There is the concurrent release of foaming constituents together with anti-foaming agents. It is apparent that the concentration of these components in the plant, their relative rate of release into the rumen, and the rate of modification by microbial action will all be of some importance.

After the animal has bloated to a certain stage, belching often ceases and hence a secondary effect due to pressure or toxic factor may be taking over. In very severe bloat the release of gas from the foam by dosing with anti-foaming agents does not always mean that the animal can eructate as at an earlier stage. Moreover, some animals appear to be able to tolerate considerably greater pressures than others without death ensuing. This critical stage at which animal reaction can mean the difference between recovery and death needs further investigation.

CAUSE OF DEATH

The cause of death from bloat has not been adequately investigated due mainly to the difficulty of obtaining clinical cases at the right stage. Dougherty, Meredith and Barrett (1955) who recently determined the physiological reactions occurring in acutely insufflated conscious sheep suggest that tissue anoxia plays an important part in the terminal symptoms, but consider that the circulatory and blood gas changes cannot be entirely explained on the basis of the simple mechanical influences elicited during increased intra-ruminal pressures. Dougherty and Cello (1952) have postulated that toxic substances in rumen ingesta might be a contributing factor in causing death.

Phillipson (personal communication) has studied the effects of distension of the rumen of anaesthetized sheep with carbon dioxide, oxygen and nitrogen, on blood pressure, respiration and blood flow through the rumen wall. He found that carbon dioxide caused an increase in the ruminal blood flow and hence distension of this organ in bloat means that the blood flow is maximal until pressure becomes great enough to impede it mechanically. This also implies that the most favourable conditions are present for rapid absorption of any soluble material in the rumen. Phillipson feels, however, that from his experiments there is no reason to reject the hypothesis that death from bloat is due to anoxia (see also Kay and Phillipson, 1959).

PREVENTION AND TREATMENT OF BLOAT

PREVENTION, GENERAL

There are many theories held by agriculturalists as to the best ways of avoiding bloat These include not pasturing the herd when dew or frost is on the grass cutting and wilting the herbage, and keeping the animals full so they will not graze a lush pasture ravenously Though these may reduce the incidence of mild bloat on mildly toxic herbage, severe bloat can certainly occur even when these precautions are taken The feeding of hay before pasturing has been widely advocated but is not always found to be effective Cole *et al* (1956) have stated that Sudan hay was the only roughage they studied that was completely effective, and it had to be supplied overnight if the cows were to eat enough to be protected When cows had access to hay for only two hours before pasturing they consumed 14 lb This amount protected most animals but not all Very leafy hays such as fine-stemmed lucerne were not effective even though considerable amounts were consumed

GRAZING CONTROL

Various methods of grazing control have been tried with the object of (1) restricting the selection of clover and particularly the succulent tops, which are believed to be more potent than the remainder of the plant, and (2) altering the grazing pattern and reducing the rate of intake to such a level that the animal is able to cope with potent material

Control of selection has been achieved by herbage cutting and stall feeding, or by making the animal eat the whole plant by use of an electric fence (Sears, 1953) Under this latter system the herd of cows is intensively grazed on a number of strips or 'breaks' of pasture during the day Though both these methods may reduce the number of cases of mild bloat, they most certainly do not give full control of severe bloat without a reduction of food intake (Reid, 1956)

Hancock (1954) attempted to change the grazing habits of cows Arguing that bloat may be due to the period of intense grazing after milking it seemed that a measure of prevention could possibly be achieved by offering the cows one half of their daily allocation of pasture before the morning milking and the other before the afternoon milking However, as found also by Johns (1954) the oft-stated opinion 'bloat is caused by greedy eating of dangerous pasture' was

not substantiated and the method showed little promise. Hancock also tried a system of 'on' and 'off' grazing to break up the grazing pattern. This showed some promise but was time-consuming and had other drawbacks.

PASTURE MANAGEMENT

As bloat is primarily an ailment associated with the ingestion of legumes the long-term aim in a programme of bloat control should be to achieve grass-dominant pastures. Clovers are an essential component of our swards and hence cannot be eliminated. The aim should be to reduce their intake to safe levels by diluting them with harmless herbage. The safe proportion of potent clover will always be difficult to define as it will depend on the potency of the clover, the palatability of associated grasses and the selective grazing habits of the animals. Troughton (1955) produced bloat in his grazing trials with clover levels as low as 33 per cent of the sward and this also occurs under New Zealand conditions. A common farm practice based on the dilution method is to graze the cows for a short period on dangerous pasture and then remove them to safe food such as rough pasture, autumn-saved pasture, crops or silage. This system entails constant supervision of the grazing animals.

ANTI-FOAMING AGENTS

The use of anti-foaming agents appears to be a logical method of preventing frothy bloat. It was found in stall-fed animals (Johns, 1954; Reid and Johns, 1957) that frothy bloat could be prevented by the administration of anti-foaming agents before feeding on clover. These agents were administered as drenches or mixed with small amounts of dry food and gave complete protection from bloat for the succeeding two hours. It had been hoped that such a measure would protect the animals from morning till evening milking, but even increasing the dose did not give protection consistently for this period. However, the method of feeding an anti-foaming agent with meal in the milking shed has been used with some success by farmers in South Africa and New Zealand who only feed the dangerous pasture subsequently for a restricted period.

It appears that the anti-foaming agents used are lost rapidly from the rumen and hence the only reliable method would be to have a continuous intake with the food. Clark and Weiss (1952*b*) suggested spraying with a weak solution of a proprietary anti-foaming agent.

Reid (1955, 1958) has successfully developed the method of pasture spraying for bloat control using emulsified vegetable or mineral oils or emulsified tallow (see also Johns, 1959) This method has been used very widely in New Zealand and Australia to give complete control over outbreaks of bloat economically Another method of administering anti-foaming agents which has met with moderate success in the field has been the use of oil on the water troughs This is more effective in dry weather and where the cows do not have access to other water

It has been found that various types of silicones with and without dispersing agents have not proved as reliable or effective as the oils in preventing bloat (Reid and Johns, 1957)

PENICILLIN

Barrentine *et al* (1956) found that orally administered penicillin controlled bloat in the field Doses of 50 mg of procaine penicillin gave good protection from bloat in yearling steers for 1 5- to 3-day periods Older animals required 50–70 mg to prevent them from bloating Penicillin had to be given several hours previously or overnight before it was effective in preventing bloat in animals that were bloating before treatment Percival (private communication) has not found penicillin as effective in controlling bloat as Barrentine In unpublished work from this laboratory we have used 100–200 mg of procaine penicillin and obtained very good control of bloat for 2–3 days after dosing There are indications, however, that the bacterial flora may become resistant to the treatment after a period of repeated dosing (Mangan *et al*, 1959) Work has shown that the penicillin acts by slowing down the initial rate of volatile acid and gas production and reducing the foaming properties of the rumen contents After treatment, food consumption may be slightly higher than before. No detrimental effect has been found on the quantity or quality of the butterfat, nor does any penicillin appear in the milk.

One of the chief difficulties in the use of the treatment, apart from the possibility of resistance developing, is the administration of penicillin to the animals It can be fed in a concentrate ration, but many animals will not eat it unless they are accustomed to taking such a supplement. We have used the dosing of capsules with a 'balling gun', but the method is hardly practicable with a large herd Barrentine *et al* (1957) have used a penicillin and salt mixture containing 50 mg of procaine penicillin per ounce of salt with considerable success How-

ever, in some cases it may not be easy to obtain a reasonably uniform distribution of penicillin throughout the herd by this method. Further research on the use of penicillin is needed before we are certain that we know all the implications of the use of this prophylactic.

There appears to be no method at present of preventing the occasional loss of cows from bloat. However, the use of oil spraying or penicillin can overcome major outbreaks of the trouble by allowing a farmer to graze dangerous pasture and hence permit other bloat-potent fields on his farm to mature.

TREATMENT

The value of anti-foaming agents in the treatment of bloat depends on the proportion of cases that are of the frothy type. Clark (1948) believes that most cases in South Africa are in this category or partially so and Battentine considers that the pasture bloat encountered in the Mississippi Basin is due to foam in the rumen. Our experience in New Zealand is that the great majority of cases respond to anti-foaming agents.

Vegetable oils, paraffin, turpentine, cream, etc. have been successfully used in relieving bloating animals by drenching. Such commonly used substances as turpentine and certain phenolic compounds have been shown by Clark (1948, 1950*b*) to owe their efficacy to their anti-foaming properties. Quin *et al.* (1949) claim success in the treatment of bloat with methyl silicone preparations though the use of collateral treatment makes it difficult to judge the efficacy of the method. Reid and Johns (1957) have found that the silicones are not as reliable as the vegetable oils. Nichols (1954) has used some household detergents and surface-active agents to clear the rumen of froth. The only detergents that we have found effective in deflating bloating animals are the non-ionic 'Pluronics' manufactured by the Wynadatte Chemical Company in the United States. When used at the rate of 1 oz. per animal Pluronic L61 or L62 has the added advantage of protecting the animal from bloating for 24 hours. The use of antihistaminics as suggested by Kerr and Lamont (1946) was found by Johns and Reid (1954) to be definitely dangerous in the treatment of frothy bloat but antihistaminics have a place where an allergic reaction is involved. In cases where bloat is chronic, the use of such treatments as antibiotic therapy (Chivers, 1954) or calcium therapy (Rydell, 1955) may be indicated. Such methods as standing animals uphill, a gag

in the mouth or driving animals around the field are often used and are sometimes helpful but are not always reliable

Anti-foaming agents are useful where the animals are not in too distressed a condition, but in an acute case where prompt relief is essential, the trocar or knife appears to be the safest remedy If only a small pocket of gas is present a considerable incision may have to be made to remove solid material that blocks the opening The usefulness of an anti-foaming agent administered through the trocar is problematical for if the animal is in such a condition as to warrant the employment of this instrument, speed is the essential requirement if the animal is to be saved

CONCLUSIONS

Research on bloat during the last few years has at least made more obvious the complexity of the problem Neither the animal nor the plant factors involved can yet be defined though some logical control measures are now available The answer will come from a filling of certain gaps in our knowledge of ruminant physiology, plant biochemistry and the microbiology of the rumen It is becoming more and more apparent that problems such as bloat cannot be investigated with much chance of success by scientists of one discipline It is necessary for animal and plant physiologists, biochemists and microbiologists all to make their contribution

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CHAPTER FOURTEEN

Ketosis in Cattle

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Introduction—Incidence and seasonality—Aetiology—Ketosis and hypomagnesaemia—Treatment—Conclusions

INTRODUCTION

Ketosis or acetonaemia can hardly be classed as a disease which is a direct result of grazing or pasture management. Nevertheless it was considered worthy of mention because of the many resemblances it bears to pregnancy toxaemia of the ewe and of the fact that management of the dairy cow, either in winter or summer, may be directly related to pasture management and to the use and quality of conserved pasture products. This chapter is not, however, an exhaustive review but rather a comment on our present state of knowledge: for an exhaustive treatment of the subject the reader is referred to Pearce (1960) who discussed the subject of ketosis in all animals with special reference to cattle.

The presence of more than trace quantities of ketone bodies in the blood, urine and milk of dairy cows is a frequent biochemical finding. It may occur without detectable clinical symptoms, other than a 'ketone' or 'acetone' smell in the breath, or in association with a condition known variously as ketosis, acetonaemia, acetonuria, acidosis, ketonaemia, slow fever and other synonyms. The condition is usually non-febrile and mortality is low. Despite extensive investigations in several countries, there remains much to be learned concerning the aetiology of this condition and of the physiological and biochemical changes in the affected animal. Similarly the relationship of ketosis

to pasture and to pasture products calls for further study, although the disease occurs most frequently in housed animals fed conserved products and is much less common in dairy cows at grass

Udall (1936) discussed the symptomology of ketosis in considerable detail and indicated that the condition had been described in Europe at least as early as 1849 He defined it as 'a parturient or non-parturient disease of well-nourished, high producing cows of all ages characterized by a marked hypoglycaemia, acetonuria and acetonaemia, thought to be due to an impaired carbohydrate metabolism' Symptoms include depression, sometimes motor irritation, paresis, rapid loss of condition and a sweetish acetone like odour in the breath, urine and milk. There is frequently a sudden and marked fall in milk yield, a loss of appetite especially with regard to concentrated food and sometimes an apparent craving for roughage

Udall distinguished between parturient and non-parturient types, and recorded approximately equal numbers of each He recognized at least three clinical types, which overlapped somewhat, viz. a milk fever or paresis syndrome a digestive type, and a nervous form manifested by excitation, delirium, motor irritation and paraesthesia. In commenting upon Udall's classification, Blood (1956) reported from New South Wales that in his own series of 152 cases there was a continuous range from the animal with a simple indigestion-like syndrome to the animal with purely nervous symptoms The milk-fever type be found to occur during the same period as that at which milk-fever itself occurs, and believed that the two conditions occurred simultaneously

Despite its sometimes alarming symptoms, neither Udall nor other authors report a serious mortality from primary ketosis—a term used to distinguish the condition under discussion from the secondary ketosis that may accompany such conditions as metritis, pneumonia and foreign body reticulitis, and that it is much more common than is generally supposed, hence causing considerable confusion in diagnosis and treatment (see Sampson and Hayden, 1936, McBarron, 1952, Dukes, 1955) Very few primary ketosis cases die, and in those that do it is probably some complicating factor which is responsible. Spontaneous recovery, heralded by normal dunging and a return of appetite, is the rule, and this makes assessment of treatment difficult. Presumably many allegedly successful treatments owe their reputation to recoveries that would have occurred anyway Although these frank cases are associated with trouble and productive loss, it is con-

ceivable that mild, unrecognized or even sub-clinical cases may in the aggregate be of even greater economic significance.

Scandinavian workers have distinguished between 'small farm acetonaemia', or that associated with underfeeding, and 'estate acetonaemia', associated with relative overfeeding. Carlstrom (1950) reported that the former occurs almost exclusively during the later part of the stall-feeding period, but varies in frequency from year to year, being particularly high in those years in which the quality of the straw is poor. Estate acetonaemia tends to occur during the early part also of the stall-feeding period; it appears to be associated with a high plane of nutrition immediately before and after calving, and attempts to find a qualitative deficiency in the diet have not been rewarding.

An important finding from the work of Breirem, Ender, Halse and Slagsvold (1949) was that relating to the method of feeding after calving, i.e. that there should be a gradual and smooth increase. 'An irregular and rapid increase may lead to inappetance and "going off feed", which secondarily may cause metabolic diseases. It is necessary to be especially careful with voluminous feeds, for instance silage.' They compare their findings in this respect with those of Shaw (1947) on the effect of palatability of rations. Since mortality is low, the economic importance of ketosis lies chiefly in its effects on milk yield, which is reduced considerably during the course of the disease and seldom reaches its anticipated level during the remainder of the lactation. It is difficult to assess the extent of this loss although Shaw (1955), in a comprehensive review of the disease as encountered in herds in the United States of America, estimated that the loss of milk represented a loss of ten million dollars per annum to the dairy industry in that country and that about a million cases developed annually. A secondary and contributory effect on losses is the culling or disposal of cows which fail to respond to treatment or which lose condition and milk thus rendering them uneconomic for further production.

INCIDENCE AND SEASONALITY OF OCCURRENCE

Recent surveys in England, Scotland and Wales (Leech, Davies, Macrae and Withers, 1960) and in Northern Ireland (Gracey, 1960) have indicated that the incidence of ketosis has a serious effect on the economy of dairy farming. Leech *et al.* estimated that the incidence was between 0·9 and 3·8 per cent in the eight areas surveyed and was higher in the north than in the south and south-west. Also, the

incidence of ketosis changed markedly in successive lactations, increasing from 0 6 per cent in the first lactation to 3 1 per cent in the fourth when it declined slightly The greatest number of cases reported occurred from December to March the seasonal minimum of ketosis was in June but 93 per cent of the cases occurred in the winter period from October to April Ketosis occurred more frequently in the Ayrshire breed (2 6 per cent) followed by the Channel Island breeds (2 1 per cent), and 62 per cent of cases occurred in the first four weeks after calving The incidence was higher in large herds than in small herds In the Northern Ireland survey ketosis accounted for 3 3 per cent of all deaths (which amounted to 1 2 per cent of a sample of nearly 7,500 animals) recorded in milch cows and for 0 4 per cent, and 0 6 per cent of sickness in 1954 and 1955, respectively

During the war years there was a marked increase in ketosis in Norway Breirem *et al* (1949) recorded data from cow testing stations in Eastern Norway based on between 6 000 and 7,000 animals each year The incidence varied from 18 0 to 88 6 cases per 1,000 animals each year and was associated with war-time rations characterized by a low content of protein and readily available carbohydrate as well as being deficient in phosphorus and B vitamins Cases were most frequent during the latter part of winter

In some high-yielding herds the frequency of both ketosis and hypomagnesaemia was disturbingly great, and on some farms every second cow was affected Ketosis predominated especially during the months of January to May In the war years less hay was used and feeding with oil-cakes was entirely suspended these being replaced with cellulose and herring-meal The amount of silage was often largely increased The quantities of roots were augmented during the first two years of war, but thereafter fell to below the pre-war level (Breirem 1943) The war-time rations were characterized by low contents of energy, protein phosphorus and readily-soluble carbohydrates and the B vitamins in particular, were below normal. Although there was an overall protein shortage, many of the high yielding cows received adequate quantities of it at the expense of those in the less productive stages of lactation. Since there was a concurrent deficiency of energy the protein content per Scandinavian feed unit was often higher than normal for the high-yielding cows Ender, Halse and Slagsvold (1948), in their survey of feeding in herds affected severely with hypomagnesaemia, showed that low calorie normal protein ratios were common in such herds at the time of the

outbreaks. At the Agricultural College of Norway there were no recorded cases of ketosis in the herd prior to the war, whereas Breirem (1943) recorded that up to 35 per cent of the cows showed symptoms. In the years following the war there were again no cases (Breirem *et al.*, 1949).

A seasonal incidence of ketosis has been demonstrated in both pre-war and post-war conditions in the United Kingdom. Eden and Green (1940), reporting on observations made during 1937–8, compared the blood pictures in a dairy herd of 59 cows at grass during the summer of 1937, in stalls in the late winter of 1937–8, and again at grass in the summer of 1938. In 70 per cent of the herd there was a marked rise in blood ketone values during the winter months, the average winter value being 8·1 mg. compared with a summer value of 3 mg. per 100 ml. In 30 per cent of the animals during winter, the level lay between 5 and 10 mg., one animal attaining a value of 45 mg. per 100 ml. There was no associated hypoglycaemia, acidosis, or alteration in the plasma bicarbonate values. Although correlation of blood ketones bodies with the period of lactation and the quantity of concentrates allowed for milk production was not pronounced, it was sufficient to indicate that high-yielding cows were more susceptible. Mackay (1943) reported that the peak incidence of acetonaemia in Cumberland was in February and March, and that where the cow could be turned out to grass, recovery was uneventful.

Holmes (1950) confirmed the existence of a high incidence of sub-clinical ketonuria in a herd of 40 lactating Ayrshires in the Wirral between January and June, 1948. The incidence was higher in cows than in heifers, and was much higher in the early months of the year when the animals were stall fed. It fell almost to zero when the animals were turned out to spring grass.

Boddie (1949) referred to an unspecified number of samples he had examined at regular intervals from cows in various parts of Scotland, and recorded a progressive increase in the ketone content of the blood and urine throughout the winter in dairy but not in beef cows. Boddie referred also, without providing experimental details, to his work on the production of substantial quantities of ketones from the suitable incubation of the washing from rumen contents from cows in late winter with turnips.

McEwen and Foggie (1950) suggested that factors other than dietetic might help to account for the rapid disappearance of ketosis in cows turned out to grass in spring. 'After the close confinement of the

stall the freedom of movement at pasture might well be expected to stimulate metabolism, and, coupled with access to appetizing food, this freedom may be reflected by enhanced bodily fitness and recovery from ketosis.' They applied the Rothera test to milk samples obtained from comparable cattle from predominantly arable farming areas of East Scotland either tied up in stalls or housed in courts formerly used for store cattle. In this court system of dairying the cows were tied or yoked during milking and feeding, but at all other times were free to move within the confines of the covered court. In 1948–9 a significantly greater number of positive reactions was obtained in samples from byre herds than occurred in samples from court herds, and there were more cases of clinical acetonaemia among the byre cows.

The relationship of pasture to clinical or subclinical ketosis is discussed in a number of publications from the United States. Duncan, Huffman and Tobin (1939) describing their attempts to treat an outbreak in a herd that was on a poor quality soybean hay, maize, silage and grain ration, reported that in some cases the condition persisted throughout the remainder of the winter, but cleared up once the cows were turned out to pasture.

Knodt, Shaw and White (1942) recorded a marked elevation of blood and urinary ketones during the late winter and early spring months in animals receiving molasses-treated grass silage, whereas the lowest concentrations in these same animals were observed when they were on early spring and summer pastures and were receiving grain, hay and a relatively small amount of silage. Because the feeding of fresh silage did not result in a similar effect, it was considered that the ageing of the silage was responsible. McBarron (1952) reported acetonaemia in New South Wales on pasture between December and March, when there was a scarcity of green feed, and one outbreak on short pasture during September, recovery from which may have been assisted by a rapid growth of the herbage.

Talsma (1952), who considered that the feeding of silage containing large quantities of butyric acid is of considerable aetiological significance, brought forward evidence from Holland that supports the views of McEwen and Foggie (1950). When cows suffering from acetonaemia were exercised for from 30 to 60 minutes, the total blood acetone body content fell from an average of 28.7 to one of 22.4 mg. per 100 ml. and during this time the average blood glucose level rose from 30 to 50 mg. per 100 ml. He stated that these facts were in agreement with the experience in the Netherlands where developing cases of

acetonaemia recovered quickly on pasture due to exercise, so that the condition was rarely seen in summer.

Clinical cases do, however, occur in the summer months even when exercise or pasture is available, as has been recorded from Jersey by Messervy (1943).

In assessing the influence of pasture, silage or other factors upon either frank acetonaemia or the occurrence of the biochemical findings without clinical symptoms, due regard must be paid to possible other seasonal factors. In the United Kingdom, the introduction of the winter milk bonus in 1940 helped to spread the incidence of calving in those areas that were geographically suitable—as is discussed elsewhere in this book. Prior to that date the incidence of spring calving was higher than that of autumn calving, and cows pregnant during the winter months or initiating their lactation in early spring would be subjected to a double metabolic and seasonal stress not dissimilar to that imposed upon the majority of ewes. The high proportion of spring calvings would in any event have implied a seasonal occurrence of parturient acetonaemia.

AETIOLOGY

In a disease which is so obviously associated with a physiological dysfunction many suggestions have been made regarding aetiology and the factors associated with occurrence. These include a dietary deficiency such as deficiency or imbalance of carbohydrate intake, a high-protein diet and a low-protein diet. This disease has been associated also with vitamin deficiencies including members of the vitamin B groups and vitamin A. Cases have also been related to mineral deficiencies including deficiencies in calcium phosphorus, cobalt, manganese and copper. Rumen dysfunction, resulting from faulty nutrition or from a sudden change of ration involving a decreased or abnormal production of volatile fatty acids or even the production of ketone bodies in the rumen itself, has also been postulated. The effect on the bacterial population and the resulting decrease in the production by the rumen flora of members of the vitamin B complex has also been considered as a possible contributory cause. The interest and use of corticosteroids in medicine and the postulates of Selye (1946) have focused attention on the possibility that an endocrine deficiency and imbalance may be concerned in the aetiology of ketosis involving the pituitary, the pituitary-adrenal cortex system or even the thyroid in relation to other endocrine glands. Finally, hepatic dysfunction,

resulting from fatty infiltration, has also been suggested as one of the primary lesions which results in the precipitation of symptoms These and other factors are dealt with by Pearce (1960) The incrimination of silage, mentioned elsewhere in this chapter, is worthy of comment, and was in fact investigated experimentally by Brouwer and Dijkstra (1938), who reported ketonuria and somewhat higher urinary ammonia levels in a grass-silage fed group of cows as opposed to a grass-hay fed group When the feeding regimes were reversed, ketonuria disappeared from the first group but appeared in the second

More recently, Adler, Roberts and Dye (1958) have demonstrated the presence of ketone bodies in grass silage, and in one instance in maize silage, they believe that a relationship exists between the ketone body of the silage and the incidence of ketosis, probably because ketogenesis is related to butyric acid production. However, as Pearce (1960) stated, although silage feeding is sometimes a precipitating factor, it cannot account for a large number of cases The study of ketosis is handicapped by the fact that it is difficult, or impossible, to reproduce it in cattle at will under closely controlled experimental conditions Shaw (1946, 1947) produced a fasting ketosis in dairy cows, as did Breirem *et al* (1949) in Norway and Robertson and Thin (1953) in Scotland Brown (1953), reporting on his studies with fasting cows, stated that the low volatile fatty acid content of rumen fluid, frequently observed in cows with ketosis and the relatively lower amounts of propionic and butyric acids were duplicated by witholding feed from normal cows for 15 to 20 hours, and considered that data obtained from cows with ketosis should be compared with data from fasted cows for proper evaluation

There are, however, undoubtedly differences between fasting ketosis and ketosis as recognized clinically, which was not induced by the various workers already cited or by Leffel and Shaw (1957) in their studies using different levels of protein and energy intake

The investigator has, therefore, to depend for his research material on naturally occurring cases of the disease and to relate his experimental observations to one or other of the various factors already mentioned, which are more probably contributory and may bear no direct relationship to the basic physiological or biochemical lesions. Recently, however, there have been advances in our knowledge of the basic aetiology of ketosis in man and animals which should undoubtedly be of significance in attempts not only to treat but also to prevent the condition in cattle

In ketosis the level of ketone bodies, which are present under normal conditions in the blood in small amounts, is raised. The ketone bodies normally present are β-hydroxybutyrate, acetoacetate and acetone and, in cases of ruminant ketosis, iso-propanol (Robertson, Thin and Stirling, 1950). In the chemical sense of the word, of these only acetoacetate and acetone are ketones, but β-hydroxybutyrate and iso-propanol are closely related to acetoacetate and acetone respectively and are readily converted to the corresponding ketones *in vivo*. Many tissues can utilize ketones as a source of energy breaking them down to carbon dioxide and water. Recent work by Williamson and Krebs (1961) has shown that acetoacetate is, in fact, the preferred source of energy for the intact rat heart and for several other tissues including amongst others sheep heart homogenates *in vitro* (Kulka, Krebs and Eggleston, 1961).

The ketone bodies arise from two major sources, either directly or as a result of rumen fermentation. In the course of the latter fatty acids such as butyrate and propionate are formed, the former being converted in the wall of the rumen to β-hydroxybutyrate, or from the breakdown of fatty acids. When fatty acids, arising either from absorption from the rumen or from the breakdown of fat, are metabolized this leads to the formation of acetyl co-enzyme A and in certain cases directly to acetoacetate. In normal conditions most of the acetyl co-enzyme A combines with oxaloacetate to form citric acid, which is then broken down to yield energy through the various stages of the tricarboxylic acid cycle and regenerates ultimately more oxaloacetate. Acetyl co-enzyme A can also condense to form acetoacetyl co-enzyme A and then acetoacetate or to form fat by a series of condensations. Acetyl co-enzyme A can thus be seen to play a central rǫle in metabolism. The accumulation of acetyl co-enzyme A leading to the formation of ketone bodies could be due either to an over production of acetyl co-enzyme A or an under utilization of it. If, in fact, there is under-utilization of acetyl co-enzyme A this would be due to a lack of oxaloacetate with which to condense. It has been shown *in vitro* that there is accumulation of ketone bodies when there is a lack of oxaloacetate (Lehninger, 1946). Similarly dietary ketosis induced by the feeding of butyrate can be reduced by the administration of oxaloacetate and substances thar can act as precursors for oxaloacetate (Beatty and West, 1951; Fasella, Baglioni, Turano and Siliprandi, 1958). The ketosis of human diebetics and of cattle suffering from bovine ketosis is not however influenced to any extent by oxaloacetate or its

precursors (Mackay, Sherrill and Barnes, 1939, Dunlop and Arnott, 1937, Lawrence 1937; Dibold, Frey and Lapp, 1937). This indicates that in these conditions there is no under-utilization of acetyl co-enzyme A but rather over-production. Fasella *et al* (1958) have concluded from this that diabetic ketosis and dietary ketosis are fundamentally different. Krebs (1960) is more cautious and prefers to express this difference by the statement that different factors limit the formation and utilization of acetyl co-enzyme A in these two conditions.

The accumulation of intermediary products such as ketone bodies is a most unusual occurrence in animal tissues. Normally, as has been demonstrated experimentally, once a substrate molecule of respiration starts to be metabolized it is used completely before a new molecule is attacked. Inhibition due to the presence of metabolic intermediates does not seem to occur in the state of ketosis where the presence of acetyl co-enzyme A or ketone bodies does not suppress the degradation of further substrate molecules. Why this should be so is still a matter of speculation, though the fact that ketosis can be induced by anterior pituitary extracts suggests that the co-ordination of acetyl co-enzyme A production and utilization is under hormonal control of the pituitary gland.

Further light has been thrown on the aetiology of ketosis in cattle by the observations made by Bach and Hibbitt (1959) on a series of clinical cases in Jersey cows. These workers examined blood samples for a variety of substances including pyruvate, citrate, alpha oxoglutarate and succinate as well as 'ketones' and blood sugar, and compared the values with those found in clinically normal cows. As well as noting a relationship between the degree of ketonaemia and hypoglycaemia they found that, in ketosis, the pyruvate and α-oxoglutarate were higher than normal and that there was a marked lowering of the citrate and succinate levels. Their observations suggested the existence of an interference within the citric acid cycle in the pyruvate to citrate and α-oxoglutarate to succinate paths and a deficiency in a co-factor such as co-enzyme A. Their results would indicate a blockage in the tricarboxylic acid cycle although this reduction was not noted by Krebs (1960). This divergence may merely be an expression of the differences between monogastric and ruminant animals for, in the latter, ingested carbohydrate is not absorbed direct but mainly as acetate with an increased requirement for co-enzyme A. On the results of their work Bach and Hibbitt were able to postulate that the diversion of co-enzyme A as acetyl

co-enzyme A to the mammary gland for the synthesis of milk fat (and the demand would reach the peak in early lactation) would result in a temporary deficiency of the co-enzyme in the citric acid cycle.

Ford and Boyd (1960) in a limited number of clinical cases, studied the relationship of fatty infiltration of the liver not only to clinical symptoms but also to various blood constituents. Their observations indicated that, at the early stages of the disease, there was an intense fatty infiltration of the liver. These findings conflicted with earlier observations (see Shaw, 1955) in which it was concluded that the liver fat of cows during the early stages of ketosis was normal and that extremely fatty livers occurred in the later stages of the disease, suggesting that this change was due to fasting. Ford and Boyd noted in some of their cases a high serum glutamicoxolacetic transaminase level as an accompaniment of clinical symptoms, but with no change in the serum glutamicpyruvic transaminase, and they related increased serum isocitric dehydrogenase and lactic dehydrogenase with elevated blood ketones rather than with clinical symptoms. They suggested that this acute and intense fatty infiltration of the liver might result in an increased release of enzymes from the affected liver cells and might be accentuated by increases in cellular enzyme activities.

It is evident that the precise metabolic lesion in bovine ketosis has not been fully elucidated. It is evident also, however, that the more fundamental nature of observations carried out on this disease during recent years have been more rewarding than earlier observations of a more empirical nature, and more likely to produce results of a practical value. Advances in this field, as in that of pregnancy toxaemia in the ewe, will depend primarily on an increased knowledge of the normal physiology and biochemistry of the ruminant.

KETOSIS AND HYPOMAGNESAEMIA

The findings of Breirem *et al.* (1949) have already been discussed. There have been several other observations that tend to support the association of ketosis with some forms of hypomagnesaemia. In the first of their important papers on metabolic disorders in dairy cows in some New Zealand districts, Swan and Jamieson (1956*a*, *b*, *c*) concluded from a survey that uncomplicated acetonaemia was a relatively rare condition in that country, but that a mild to moderate ketosis was frequently associated with grass staggers, and that those simple cases of ketosis of which they had full individual records were all past the twelfth day of lactation. The youngest cow whose age is known was

a nervous case, a four-year-old The cow that was furthest from calving (7 months) developed the condition in mid-summer All the others occurred in late winter or spring, when pasture growth was young and fresh, but scanty in amount

In Great Britain, Dawson (1955) drew attention to the frequent occurrence of hypomagnesaemia and of acetonaemia on the same farms, and Gould (1958) stated that ketosis was often a sequel of milk fever or of hypomagnesaemia and was particularly common when heavy silage feeding was indulged in and especially when the silage was of low quality and the milk potential of the cow was good Gould stated that he was satisfied that the feeding of an adequate ration of good hay, together with feeding of production ration for half the maximum expected daily yield during the last week of six weeks, gradually increasing during 'steaming up was of considerable value in the control of ketosis He stated also that mineral supplements, of up to 2 to 4 oz. daily throughout the year were particularly indicated when large quantities of silage were being fed

TREATMENT

The therapeutics of acetonaemia are only of indirect significance to this book and certainly the literature indicates a wide choice of materials that have been advocated for the purpose.

In a disease of unknown or obscure aetiology treatment must remain to a large extent empirical or non-specific The comparative evaluation of methods of treatment is difficult in that no individual case of ketosis can be considered directly comparable with another and that such variables as breed, age and parity of the cow, milk yield and milk quality, good quality and food intakes render interpretation of results difficult Again, it is difficult to compare observations where recovery is based largely on clinical appraisement or biochemical resolution and not on eventual performance in regard to milk yield the marked reduction of which is the major cause of concern to the agriculturist Nevertheless certain treatments appear to give good results under farm conditions although observers have realized that a treatment giving good results in one herd may not necessarily be equally successful in another

The oldest category of treatment is the administration of soluble carbohydrate either parenterally, generally by intravenous injection or by mouth. The latter method is not generally recommended because an already abnormal rumen digestion may be further disturbed Such

treatment results in a temporary correction of the hypoglycaemia during which period the basic metabolic lesion presumably resolves. It is often necessary to repeat the glucose administrations. Glucogenic substances such as propylene glycol and glycerol have both been reported of value given by mouth as have salts of volatile fatty acids such as soluble lactates (see Worden and Reid, 1958) and sodium propionate. These types of treatment are often reinforced by glucose injections rendering their therapeutic assessment difficult.

Inorganic substances including sodium and potassium bicarbonate and sodium and potassium chlorate have also been claimed of value. Carlstrom and Carlstrom (1950) recorded lowered serum potassium values in puerperal ketosis, and stated that the potassium content of feeds which predispose to ketosis was low. They record that the intravenous administration of 15 gm. potassium chloride in 5 per cent w/v solution gives immediate improvement. Blackburn, Castle and Drysdale (1959) used potassium chlorate at the rate of 30 gm. twice daily by mouth in 9 cases; all responded well with a return to normal blood and milk below body levels in 4 days.

The use of corticosteroids in the treatment of bovine ketosis has been reviewed by Uvarov (1959). Adrenocorticosteroid hormone (ACTH), cortisone, hydrocortisone and prednisone, prednisolone and other materials have all been reported of value alone or in combination with other methods of treatment such as glucose therapy. The therapeutic action of this group of drugs is considered to be related to their glucogenic effect, although this is probably an over simplification of their role. Although dramatic cures are sometimes elicited by these compounds, any form of therapy should be evaluated with due regard to underlying husbandry and other factors, and with some of the more potent agents care may be necessary. Thus the work of Dye, Roberts, Blampied and Fincher (1953)—see also Dukes (1955)—indicates that cortisone can be ketogenic unless the blood-sugar level is sufficiently elevated by the same or other treatment. Chung and Shaw (1957) reported deaths in experimental goats receiving sodium salts in addition to 9-α fluorohydrocortisone, although Worden and Reid (1958) found that goats receiving 1 gm./kg. calcium sodium lactate daily could tolerate full therapeutic doses of prednisolone.

An encouraging advance in treatment methods has been made by Bach and Hibbitt (1959) who, as a logical conclusion of their biochemical studies of the disease, used sodium fumarate and cysteamine in clinical trials. Of sixteen cases treated with sodium fumarate,

14 recovered within 10 days, although the use of fumarate increased pyruvate and oxoglutarate blood levels In contrast, cysteamine therapy resulted in the recovery of 13 cases within 4 days, with a fall to normal of the pyruvate and oxoglutarate blood levels

In addition to the above methods of treatment many others have been reported, including vitamin therapy, transfusion of ruminal juice from healthy to suffering cows and exercise The evaluation of these, and for that matter, other methods of treatment is difficult and unless observations are rigorously controlled may be invalidated by the well known fact that spontaneous recovery is of common occurrence

CONCLUSIONS

Ketosis in cattle appears to arise from a variety of contributory causes, including feeding and endocrine disturbances, and is almost invariably associated with recent parturition and the concomitant demand of lactation Recent research has indicated that the fundamental lesion is an interference with intermediary metabolism involving the tricarboxylic acid cycle and the utilization of protein carbohydrate and fat These findings, taken together with the results of treatment experiments and field trials do not however allow any hard and fast recommendations to be made as yet regarding either the prevention or control of the disease There is adequate negative evidence to indicate that ketosis is of rare occurrence on good pasture although it may arise where the pasture is poor and unable to supply the demands of the post parturient lactating cow It is possible in developed countries that, with the continuing improvement of production potential of the dairy cow together with the increased life span of cattle which has resulted from improved control of infectious conditions, there may be an increased susceptibility to, and incidence of, ketosis Whatever the precise details of its aetiology, careful husbandry and what the Scandinavians refer to as gradual and smooth changes in the feeding levels would appear to be of basic importance in lowering the incidence of this rarely fatal but economically serious disorder of the modern dairy cow

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CHAPTER FIFTEEN

Pregnancy Toxaemia in the Ewe

P D S PUGH AND K C SELLERS

Incidence—Symptomatology—Post-mortem findings—Biochemical findings—Classification of the group of pregnancy toxaemias—Aetiology of pregnancy toxaemia—Studies relating to symptomatology—Treatment and prevention

In the study of animal diseases the main efforts have, in the past, been directed towards the solution of questions relating to infectious diseases However, in recent years, advances in preventive medicine, and efforts to improve animal productivity, have brought to light new disease conditions and have enhanced the importance of the well-known group of 'metabolic' diseases of farm animals One of the most prominent diseases of this group that affects sheep is ovine toxaemia of pregnancy The term pregnancy toxaemia, as used at present, probably covers more than one condition but is usually used in referring to an indifferently defined disease seen in multigravid sheep during the last three or four weeks of their 150 day gestation period Clinical signs are not strictly pathognomonic, they include nervous signs, and inappetence followed by apathy and coma The disease is fatal unless parturition or surgical removal of the contents of the uterus occurs Blood analysis shows an early and progressive elevation of the ketone body concentration and hypoglycaemia accompanied by high plasma cortisol levels and followed by a rise in the level of non-protein nitrogen and a lowered alkali reserve The main changes which have been noted *post mortem* relate to the liver which shows a fatty infiltration and a lowered glycogen content

INCIDENCE

Pregnancy toxaemia which is known by a great number of different names (e.g. pregnancy disease, twin-lamb disease) has been recognized in most areas where sheep are raised and, according to early reports, was a recognized syndrome in the last century. Its economic importance depends largely upon the fact that it affects pregnant ewes causing a high mortality rate of both mother and lambs. In a survey of the losses in certain northern counties of England, Ferguson (1953) found that 70 per cent of all deaths (equivalent to 1·9 per cent flock mortality) could be attributed to pregnancy toxaemia though the diagnostic criteria on which these figures are based are not given. Sellers and Leech (1955), estimated that approximately 2 per cent of breeding ewes in Yorkshire died during pregnancy, the greater part during the latter third (Leech and Sellers 1959); no attempt was made to diagnose the cause of death. Heath (1955) cites figures to show that pregnancy toxaemia accounts for 6 per cent of the deaths of adult ewes.

The disease occurs in ewes during the last three or four weeks of pregnancy. The ewe is generally multigravid, though cases have been reported in ewes bearing a single large lamb: for example in 53 cases reported by Roderick *et. al.* (1933) 43 ewes had twins, 5 had triplets and 5 had single lambs. It is considered that there is no breed predisposition (Roderick *et. al.*, 1933) although the disease is rare among pure bred hill ewes and commoner in lowland flocks (Lyle Stewart, 1953). In this connection, however, it is of interest that in Iceland, where there are about half a million sheep, there is little history of pregnancy toxaemia although lambing sickness occurs and ketosis is very common in cows (Lyle Stewart, 1953). The disease usually affects older sheep, in which multiple births more commonly occur (Kelly, 1939) rather than the yearling sheep or the very old (Marsh, 1928; Dayus and Weighton, 1931; Roderick *et. al.*, 1933).

The incidence of the disease is very variable from farm to farm and from year to year; in a survey in North Wales, Michael (1957) reports 827 cases out of 21,467 ewes in 1955, whereas in 1956, only 19 cases occurred among 20,607 ewes.

SYMPTOMATOLOGY

Since the work of Greig (1929) on the occurrence of acute hypocalcaemia (lambing sickness) there has been less confusion in des-

cribing the symptomatology of pregnancy toxaemia. Nevertheless, although there is still a need of accurate observation both qualitative and quantitative on the course of the disease, pregnancy toxaemia can be divided into two broad types on a clinical basis. There is a nervous form where clinical signs are pronounced over several days with coma at the terminal stage and there is a lethargic form, where a profound lethargy begins early in the condition and may last for several days.

Nervous signs are generally seen in the disease associated with overfat ewes (Clark, Groenewald and Malan, 1943; Rowlands, 1952). In the opinion of Parry (1950) there are manifestations of nervous derangement in the majority if not all cases. However, since these signs may be transient and the episodes not very clear they are often overlooked. Lyle Stewart (1952) has found that the type showing pronounced nervous manifestations of excitability is relatively rare in North England. In the cases described by Dayus and Weighton (1931), where a progressive malnutrition occurred, the apathetic type predominated.

The literature is replete with clinical reports, and it would be inappropriate to detail the various clinical signs described as characteristics of pregnancy toxaemia by various observers. Affected ewes are generally first noticed when they show signs of depression, with refusal of food and usually of water. The main nervous signs include excitability, apparent impairment of vision or blindness, unsteady and erratic gait, convulsions and periods of struggling. The breath smells of acetone, there may be excessive salivation, a frothy discharge from the nose and grinding of teeth and constipation. Emaciation rapidly follows the depression in appetite. As the condition progresses, affected ewes become more and more lethargic and eventually become recumbent in a semi-comatose state progressively becoming deeper; at this stage they may adopt unusual postures. Death occurs in from one to fourteen days although recovery may occur if lambing takes place and the ewe eats and ruminates.

POST-MORTEM FINDINGS

The post-mortem findings cannot be considered as specific and many changes can be explained as the result of inanition during pregnancy. Roderick, Harshfield and Hawn (1937) give the opinion that pathological processes are already well advanced when the clinical signs are recognized.

The main finding, although not invariable, is a marked fatty

infiltration of the liver which histologically is not accompanied by degenerative changes nor by cirrhosis even in advanced cases. However, Wright (1955) has drawn attention to the similarity in histological appearance between the liver changes seen in the starved pregnant ewe and those seen in the liver of dogs, rats and mice maintained on a choline-free diet for short periods (Best, Hartroft and Sellers, 1952). Analysis shows that, as might be expected, the fat content of the liver is greatly increased whereas the glycogen content is decreased. The vitamin A content is normal (Barron 1942). There are no fatty changes in the livers of foetuses removed from affected ewes (Roderick *et al.*, 1937).

In addition to the fatty infiltration of the liver there may be a mottled appearance of the renal and omental fat (van Rensberg, 1931) and fatty changes in the kidney and Parry (1950) found that the kidney cortex was invariably pale with yellow translucent streaks interspersed with pin-point reddish foci; the medulla was normal. Histological studies of fat distribution in the kidneys of starved pregnant sheep performed by Wright (1955) indicated that this fat was almost entirely confined to the cortical region and that fat was present in the kidney tubules. In cases of pregnancy toxaemia arising from prolonged undernutrition it is common to find gross adrenal enlargement but this feature is less common when the disease has been induced over a short period by sudden and complete fasting (Reid, 1960*a*). Changes have been recorded in other organs and tissues but neither these nor the more commonly seen changes in the liver and kidney can be considered pathognomonic.

BIOCHEMICAL FINDINGS

A constant finding in pregnancy toxaemia has been an elevation of the blood ketone body concentration, an acidosis and a decrease in the blood glucose values accompanied by abnormally high plasma cortisol concentration. No correlation has been found between the clinical syndrome and the blood concentration of ketone bodies. There is a terminal rise in the non-protein nitrogen level in the blood; calcium levels are normal. The urine contains increased quantities of ketone bodies and ammonia, but there is no glycosuria.

The values for blood ketone body concentrations during the disease reported by different authors vary and have to be interpreted with a considerable degree of latitude. First, it is often hard to say for how

long the disease has been progressing Secondly, the determination of ketone bodies is still often subject to considerable inaccuracy because it involves the measurement of a heterogeneous group of compounds which do not react uniformly to the analytical procedures commonly employed The normal ketone body values (expressed as mg acetone per 100 ml jugular blood) for the pregnant ewe with twin lambs is 3 28 ± 0 63 mg (Sampson and Boley, 1940) although higher values may be found unassociated with clinical effect (Fraser, Godden, Snook and Thomson 1939) Sampson and Boley (1940) consider that 7–10 mg per 100 ml is the critical range, above which an animal may be expected to show signs of ketosis They are of the opinion that the disease develops over a period of perhaps several weeks, furthermore it is not until the ketosis reaches a certain intensity or has affected the ewe for some time that definite signs are manifested clinically Sampson and Hayden (1936) give a mean value of 31 94 mg per 100 ml for seven ewes with pregnancy toxaemia, the same ewes 72 hours before death and after treatment had a mean blood value of 21 48 mg per 100 ml

The presence of isopropanol had been reported by Robertson and Thin (1953) Urine ketone values have been given by Sampson Gonzaga and Hayden (1933), and by Sampson and Hayden (1936) These figures, ranging from 140 to 735 mg per 100 ml give no clear indication as to whether there is any difficulty in the elimination of ketone bodies in the urine in pregnancy toxaemia Studies indicating impaired adrenal function have been made by Parry and Taylor (1956)

In the later stages of the disease there is a fall in the alkali reserve level to about two thirds of normal (Healy and Hull 1928, Cameron and Goss 1940) at least part of this acidosis will be the result of the loss of base in the urine in combination with excreted acetoacetate and β-hydroxybutyrate.

There is general agreement that the blood glucose concentration is low in the disease (Roderick *et al* 1933, Sampson and Hayden 1936), although many are cautious as to what extent the clinical signs are referable to hypoglycaemia *per se* (Clark *et al*, 1943, Hitchcock and Phillipson 1946) McClymont and Setchell (1956) are of the opinion that the blood glucose concentration, and not any other factor associated with starvation, is responsible for the clinical signs. The glucose values return to their normal concentration if parturition occurs (Sampson and Hayden, 1936) in addition the ketone

body concentration returns to normal and the glucose concentration to a normal or higher than normal value if the foetus dies in utero (Sampson and Boley, 1940; Holmes, 1953; Pugh, 1954). In the foetuses from affected ewes there is said to be no significant lowering of the total reducing sugar values, and the liver glycogen figures remain within the normal range (Underwood, Curnow and Shier, 1943). Since cortisol promotes the formation of glucose from body protein in the undernourished animal a prolonged hypoglycaemia stimulates the secretion of cortisol by the adrenal cortex. Cortisol secretion may also be stimulated by generalized environmental stresses. In view of this, and in view of the adrenal hypertrophy, that is frequently but not invariably, found in cases of pregnancy toxaemia, an abnormally high plasma cortisol level is a general biochemical feature of the disease.

The urine is acid in reaction in pregnancy toxaemia (Roderick, Harshfield and Merchant, 1933), almost certainly the result of starvation, as opposed to the alkaline reaction of normal ruminant urine. The most marked findings are an increase in the ammonia content (Healy and Hull, 1928; Sampson *et al.*, 1933) and a pronounced ketonuria. There is no glycosuria. Little change is seen in the urea content or the specific gravity although the common occurrence of albumin and casts has been reported. It is very probable that oliguria occurs followed in the terminal stages by anuria, a possible reflection of the diminished water intake.

CLASSIFICATION OF THE GROUP OF PREGNANCY TOXAEMIAS

The absence of accurate data for the differential diagnosis of this condition has led to some confusion. Ketosis has often been taken as one of the main diagnostic criteria, and the difficulties of diagnosis have been enhanced by the failure to appreciate the rapidity with which a fasting ketosis can develop in the pregnant ewe.

The susceptibility of the ewe to spontaneous ketosis is contingent upon the maintenance of pregnancy (see Sampson, 1947) except in Listerellosis (Olafson, 1940). What relationship ketosis itself may have to the disease and what bearing upon the clinical condition will not become certain until more information is available on ketogenesis in the pregnant sheep. In the ewe with ketosis two facts are widely quoted as being related to parturition, namely the clinical condition improves after parturition (Rowlands, 1952; Holmes, 1953) and ketosis then disappears.

The main interest in this condition centred for many years around the blood ketone body concentration, though ketosis need not necessarily be considered as the primary expression of an altered metabolism nor need it be assumed theoretically that a similar biochemical lesion underlies ketosis under all conditions Thus although in certain pathological states ketosis may be due to a failure of the body to utilize carbohydrate at the normal rate for example in diabetes mellitus, in the diabetes after depancreatization and in glycogen storage disease, in other cases it can result from a deficiency in oxalacetate such as in fluoracetate poisoning and under still further circumstances ketosis can be considered as a 'normal' physiological state In this latter group one can include the ketosis that follows diets low in carbohydrates, anaesthesia alkalosis excess exercise and exposure to low temperatures Indeed, recently it has become more apparent from clinical reports that hyperketonaemia accompanies a variety of clinical conditions in the ruminant other than in ovine pregnancy toxaemia and bovine ketosis Several experimental investigations concerned with pregnancy toxaemia have been concerned largely with attempts to reproduce the disease by starvation and have led to the assumption of the identity of fasting ketosis and pregnancy toxaemia (e g Hopkirk, 1934, Groenewald Graf and Clark, 1941, Sampson, 1947) Although a reduction in food intake under many conditions can lead to a ketosis (Roderick, Harshfield and Hawn, 1937, Fraser *et al*, 1938, 1939, Underwood, Robinson and Conochie 1942) which it has often been found impossible to reverse sporadic cases of pregnancy toxaemia possibly occur where there has been no obvious nutritional deficiency (Roderick *et al*, 1933, Elder and Uren, 1943, MacDiarmid, 1952) Nevertheless the opinion may justifiably be advanced that in many countries where sheep are kept on a large scale, ketosis following starvation or malnutrition is of much greater economic importance than such sporadic cases of pregnancy toxaemia

In general, the toxaemias of pregnancy make their appearance in multigravid sheep when one of two conditions prevail firstly when overfat ewes suffer sudden stress, and secondly when the plane of nutrition becomes clearly inadequate towards the end of pregnancy (Roderick *et al* 1933) Thus pregnancy toxaemia can be subdivided into two main types, nutritional and starvation with the possibility of a third group as well, which can best be called 'idiopathic' pregnancy toxaemia

Nutritional pregnancy toxaemia follows a progressive shortage of

food, mainly of a quantitative nature but possibly associated sometimes with a qualitative deficiency. It is therefore more commonly seen in ewes which are in moderate or poor condition, especially those on a relatively high plane of nutrition early in pregnancy as, for example, when much grass is available in the autumn and early part of the winter. In the cases reported by Dayus and Weighton (1931) there was a constant history of ewes declining more or less rapidly in condition at a critical stage of pregnancy. They have also noted that the disease is commoner in ewes which have been well-fed at the beginning of pregnancy which is likely to increase the eventual size of the foetus (Wallace, 1948), but where it has not been possible subsequently to maintain the condition. It may be noted that Casida (1956) showed that neither level of feeding nor twinning has a significant effect on total embryo weight before the 40th day. Further evidence for the theory that inadequate calorie intake plays an important part in the aetiology is given by Leslie (1931) and by van Rensburg (1931). The latter observer reports that in the Transvaal, drought and overstocking has impoverished vegetation and played a part in increasing the number of cases of the disease. Lack of exercise plays no direct part in this type of pregnancy toxaemia. In the Karoo areas of South Africa where the disease is most troublesome, the sheep seldom suffer from lack of exercise (Groenewald *et al.*, 1941).

Underwood, *et al.* (1943), have reported the incidence in sheep in Australia kept for experimental purposes. In two groups of 480 ewes one group on a low plane and the other on a high plane of nutrition, there was an incidence of 6·15 per cent and 10·2 per cent in succeeding years in the former group, whereas in the latter the incidence was 0·6 per cent and 1·2 per cent. In one year, a group of 183 ewes on green grazing alone showed an incidence of 7·1 per cent.

The observations quoted have largely referred to the disease as seen in South Africa, the Antipodes and the United States of America and appear mainly to be associated with under-nutrition. In Great Britain on the other hand, Lyle Stewart (1952) has drawn attention to the fact that pure bred hill ewes rarely develop the disease although they usually exist during the winter on a diet which both quantitatively and qualitatively leaves much to be desired. Ketosis in hill ewes is seen during fasting incidental to bad weather and in moss staggers. The work of Gill and Thomson (1954) is of interest in this connection. They showed that if the level of nutrition of well-conditioned ewes was reduced there was a high incidence of pregnancy toxaemia and

usually a marked ketosis, whereas in ewes which had had the same low level of nutrition throughout gestation only one case of pregnancy toxaemia occurred though some animals had marked ketosis A reduction in the ration of fat ewes for a three-week period imposed more than five weeks before lambing had no detrimental effect.

Starvation pregnancy toxaemia may be defined as a fasting ketosis following a sudden and complete deprivation of food A large number of cases may occur at the same time when there is a sudden break in nutrition, as for example after a heavy fall of snow or other disturbance preventing feeding

Idiopathic pregnancy toxaemia describes the form of the disease seen when overfat ewes are supplied with an amount of food and when there is no clear-cut explanation for the failure to eat In Britain M Fadyean (1924) first drew attention to the association of overfatness with pregnancy toxaemia Rowlands (1952) discussing the disease in North Wales says that it is commonly found among overfat, lazy ewes on restricted grazing cases occur among older ewes brought down from the mountain for cross-breeding on lowland pastures which have often acquired superfluous body fat, but have lost their native habit to wander and forage for food Cases under similar conditions have been reported from New Zealand (MacDiarmid 1952) In New Zealand the incidence of the disease has increased progressively with the subdivision of the country and the establishment of small flocks intensively fed, with little exercise (Dayus and Weighton, 1931) Although lack of exercise is popularly blamed, neither Leslie (1931) nor Dayus and Weighton (1931) consider it to be a main factor There is uncertainty concerning the reality of idiopathic pregnancy toxaemia as a syndrome distinct either from that following starvation or from the condition associated with progressive malnutrition It is possible that fat ewes in full fleece may lose weight without this being apparent to the casual observer Nevertheless, a number of cases have been reported in flocks where there is no suspicion of malnutrition and where a reason for a sudden break in nutrition feeding is not obvious

THE AETIOLOGY OF PREGNANCY TOXAEMIA

I NUTRITION PREGNANCY TOXAEMIA

Experiments have been carried out to discover whether deficiencies of either calories or protein will cause the condition

(a) *Caloric deficiency*—Reduction of food intake has been carried

out by Hopkirk (1934), Fraser *et al.* (1938, 1939), Groenewald *et al.* (1941), Underwood *et al.* (1942), Parry (1950) and others. The results of these investigations are similar. The caloric value of the diet was inversely correlated with the frequency of occurrence and severity of ketonaemia: the ketonaemia produced by under-nutrition was more frequent and severe in multiple than in single pregnancies (Fraser *et al.*, 1938). Leslie (1933) has pointed out that the average weight of twin lambs is considerably greater than the weight of a single lamb average. Malnutrition has been shown to cause some of the manifestations held to be characteristic of pregnancy toxaemia, although Wallace (1948) failed to notice any of these characteristic signs under conditions of gross malnutrition. It is of interest that the clinical signs reported by Groenewald *et al.* (1941) in South Africa and by Parry (1950) in Australia were of apparently greater severity than those reported in Britain (Fraser *et al.*, 1938, 1939).

The ketonaemia produced by these means can be ameliorated or prevented by increasing the caloric value of the diet (Fraser *et al.*, 1938, 1939; Groenewald *et al.*, 1941), which is in keeping with the field finding that cases are prevented by ensuring that the plane of nutrition continues to rise during the latter part of pregnancy. Snook (1939) showed that the fatty liver produced in experimental ewes could not be distinguished from that found in field cases of the disease. Extreme infiltration, however, can occur without clinical signs. Hyperketonaemic ewes in apparently good health were found to have livers infiltrated with fat, the nature and degree of infiltration being indistinguishable from that seen in comatose ewes. He concluded that fatty infiltration is not a normal concomitant of pregnancy in the sheep. Similar findings have been reported by Roderick *et al.* (1937). This conclusion is at variance with the usual interpretation of the findings of Dryerre and Robertson (1941). Under conditions where they could discount malnutrition or fasting, these workers showed that a rise in liver total fat, mainly by an increase of the neutral fat fraction, occurred during the third and fourth months of pregnancy reaching a maximum value of about 12 per cent total lipids. There was a marked fall in the iodine value of the fatty acids present and a decrease in the moisture content of the liver. Multiple pregnancy had no effect on this infiltration and there was no correlation between liver fat and foetal growth. Pregnancy toxaemia showed an infiltration only slightly greater than the average for a healthy ewe at a similar state of pregnancy.

Qualitatively the changes are similar. Both Parry and Groenewald

concluded that the clinical picture produced was the same, but Fraser and his colleagues were more cautious.

(b) *Protein deficiency*—Most workers are in agreement that the protein content of the diet has no effect on the occurrence or severity of ketonaemia and the effect of a protein supplement fed as a preventative is due to its calorific value rather than to any specific factor.

2 STARVATION PREGNANCY TOXAEMIA

This occurs naturally when animals are suddenly deprived of food (Fraser *et al*, 1938, 1939, Phillipson, 1950). Phillipson (1950) has made a tentative suggestion that there may be two types according as to whether the animal was previously on a high plane of nutrition or merely on a maintenance ration. He reports that sheep starved after a fattening diet showed more marked clinical signs but a lower ketone body concentration than did ewes on a maintenance ration. It may be mentioned here that in pregnant ewes deprived of food for experimental work (Pugh and Scarisbrick, 1957) no clinical condition resembling field cases of pregnancy toxaemia occurred, nor did the blood ketone body concentration approach that found in natural cases

Part of the effect of the previous diet may be in the bodily condition produced. Sheep in good condition lose weight more rapidly than sheep in poor condition (Clark *et al*, 1943) Fraser *et al*. (1938) and Groenewald *et al* (1941) found that the severity of the ketonaemia appeared to be correlated directly with the loss of body weight. On the other hand Underwood *et al*. (1942) found that starvation resulted in more pronounced signs in ewes previously poorly fed than in those which had been well fed There is general agreement that no relationship is apparent between the ketone body concentration and the severity of the clinical findings

3 IDIOPATHIC PREGNANCY TOXAEMIA

The disease which occurs when there is no apparent nutritional deficiency and when food is available If idiopathic pregnancy toxaemia can be shown to be solely a fasting ketosis of the fat ewe, then idiopathic pregnancy toxaemia is merely one form of starvation pregnancy toxaemia and the division into two distinct types is not justified The only differences would be the reason for the failure to eat To prove this identity would be of great value in furthering the study of the aetiology of the disease and subsequently the study of therapeutic measures In both the starvation and idiopathic types the

onset is relatively sudden; in the one, failure to eat is unintentional on the part of the ewe, whereas in the other, food, though available, is not eaten. No information from field cases is available to indicate whether this loss of appetite occurs before or after the development of ketosis. If the loss of appetite comes first, the ketosis can be considered as a primary fasting ketosis. There is no *a priori* reason for dismissing the possibility that ketosis itself may be a case of loss of appetite (Fraser *et al.*, 1939), as may be the case in nutritional pregnancy toxaemia, after which may follow any event which may be considered as sequels to fasting *per se.* Fraser *et al.* (1938, 1939) showed that ewes fed to over-fatness and kept in close confinement throughout gestation showed partial loss of appetite and if multigravid some degree of ketonaemia, but without clinical symptoms. Reid (1958) cites unpublished experiments by Weston which indicate that the *ad libitum* intakes of a variety of diets are the highest intakes of which the animal is capable and that appetite may be largely controlled by rate of passage of digesta from the rumen. Further observations showed that the intake of roughage in late pregnancy by ewes carrying twins is less than that of ewes bearing a single lamb. Earlier Gordon and Tribe (1951) reported that, in very fat twin-bearing ewes, the voluntary intake of food in the last month of pregnancy may fall by 20–40 per cent. This reduction in food intake may be due to marked compression on the rumen due to the large volume of the amounts of fat present in the abdominal cavity of very fat ewes (Blaxter, 1957). Reid (1958) suggests that if reduction in rumen volume lowers appetite in late pregnancy, feed intake may fall below the required level, particularly in very fat ewes carrying twins and this could explain the greater susceptibility of over-fat ewes to pregnancy toxaemia even when ample high quality feed is available to them.

There is little doubt that a preoccupation with the study of ketosis has tended to overshadow the study of the changes during starvation and from this brief account of some of the previous investigations it will be seen that the evidence is nor yet fully adequate for the unequivocal conclusion that the field and experimental diseases are the same. Nevertheless one feels justified in saying that:

(a) The conditions produced by starving a sheep at the end of gestation are the same as starvation pregnancy toxaemia.

(b) Nutritional pregnancy toxaemia resembles the condition produced experimentally by feeding a diet inadequate in calorific value.

(c) Idiopathic pregnancy toxaemia has not been reproduced 'in the laboratory' The evidence is inadequate at the moment to conclude that it is in fact a different condition from starvation pregnancy toxaemia

(d) Nutritional pregnancy toxaemia and idiopathic pregnancy toxaemia become complicated always by a fasting ketosis

(e) Previous environmental factors of which the nature of the diet is one are likely to be of importance in determining the extent of the quantitative changes on fasting and any quantitative expression of the clinical picture

STUDIES RELATING TO SYMPTOMATOLOGY

The weight of evidence both from the field and from the laboratory is sufficient to make it appear highly probable that an absolute calorific deficiency is the immediate cause of pregnancy toxaemia, irrespective of whether it is a progressive deficiency due to the unmet and increasing demands of pregnancy, or whether it is a sudden and complete deprivation of food Biochemical work is at present being carried out in many laboratories in an attempt to provide a satisfactory explanation of the clinical manifestations These studies are not yet at a stage where any but tentative conclusions can be drawn, and the following comments are intended as an indication of some of the seemingly more important trends of thought

Because ruminants appear to be particularly susceptible to the development of ketosis it has been suggested that hyperketonaemia may be a reflection of the potentially ketogenic nature of ruminant metabolism The fermentation of polysaccharides in the rumen produces a mixture of volatile fatty acids, consisting mainly of acetic, propionic and butyric acids, two of which are potentially ketogenic. Glucose, which acts not only as a metabolic substrate but also as a precursor of oxalacetate necessary for the oxidation of acetate and butyrate via the tricarboxylic acid cycle, must largely be derived from propionate and by glucogenesis from protein Hence alterations in the ruminal production, or the absorption, of propionate may also affect the metabolism of acetate increasing or decreasing its conversion to acetoacetate (Jarrett and Potter, 1950) However, in view of a number of hypotheses concerning ketosis in ruminants which are based upon alterations in the proportions of volatile fatty acids produced in the rumen and upon ketogenesis from these acids, it should be

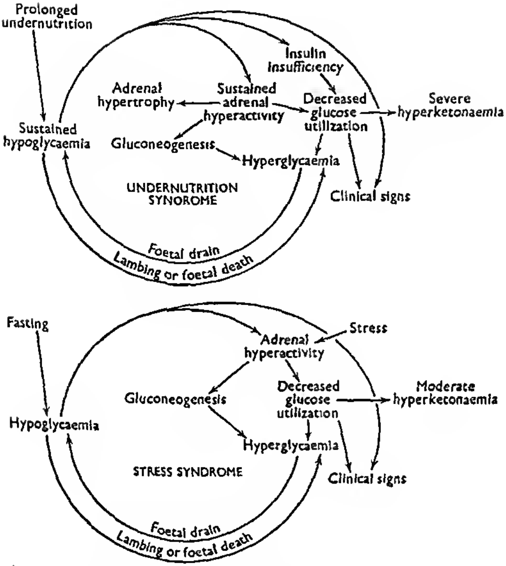

FIG 15 1 Major physiological and biochemical events in the two principal pregnancy toxaemia syndromes (Reid, 1960*b*, *Aust J Agric Res* II, 364)

emphasized that there is no evidence to show that any appreciable quantities of volatile fatty acids are absorbed during starvation (Reid, 1950, McClymont, 1951) The position is exacerbated during pregnancy by the fact that the sheep foetus does not derive much of its energy requirements from the oxidation of acetate (Pugh and Scarisbrick, 1957) Pugh (1953) produced evidence to show that hyperketonaemia in the fasted pregnant ewe is not the consequence of an impaired efficiency of the metabolic steps of the tricarboxylic acid cycle in either hepatic or extrahepatic tissues. Kalnitsky and Tapley (1958) have also shown that it was not a lack of oxalacetate limiting the utilization of acetyl coenzyme A which produced ketosis and

Beatty and West (1955) demonstrated that ketosis is not ameliorated by oxalacetate precursors. The possibility remains that it is an over-production of acetyl coenzyme A that produces ketosis.

A sustained hypoglycaemia is an essential predisposing cause of pregnancy toxaemia. McClymont and Setchell (1955, 1956) have suggested that, at least in cases of pregnancy toxaemia following a sudden and complete fast, the clinical signs result from a brain dysfunction due to hypoglycaemia. Although this hypothesis was supported by the evidence of the successful treatment of early cases with glycerol by mouth or with subcutaneous glucose injections it is not sufficiently comprehensive to account for the general syndrome of pregnancy toxaemia.

Reid (1960*a*, *b*, *c*) has provided a more elaborate and generalized hypothesis which assumes that the metabolic syndrome is a 'diabetic' one. He has succeeded in relating the major biochemical abnormalities of pregnancy toxaemia (namely hypoglycaemia, hyperketonaemia, and abnormally high plasma cortisol levels) to each other and to the clinical signs, and this view is also supported independently by haematological evidence and by studies on wool-fibre nutrition.

TREATMENT AND PREVENTION

A wide variety of substances has been used therapeutically but none has proved to be really satisfactory in the treatment of pregnancy toxaemia. An examination of the literature shows that among the substances tested and found to be ineffective are glucose when given subcutaneously, intravenously, or *per os*, insulin, calcium chloride, formaldehyde, adrenalin, sodium bicarbonate, members of the vitamin B complex, wheat germ oil, normal sheep plasma when given intravenously or subcutaneously, sheep liver extract when given subcutaneously or *per os*, deoxycortone acetate and acetylcholine bromide. However, glycerol, propionate and other glucose precursors given by mouth are fully effective in restoring both the blood glucose concentration and the ketone body concentration. In general, though, this is not attended by full clinical recovery unless the ewe be treated in the earliest stages of the condition. The removal of the foetuses will, of course, relieve the condition, and appears to be the best course to adopt if ewes do not respond clinically to glycerol therapy within 24 hours. It may be necessary subsequently to drench ewes with ruminal contents from another sheep.

There is now general recognition that pregnancy toxaemia is a nutritional disease which can be avoided by the correct management of the pregnant ewe. The husbandry measures required to ensure that the nutritional requirements of the pregnant ewe are satisfied vary widely with local conditions, and therefore it is not possible to lay down any set of hard and fast rules. Moreover, because one's knowledge of the precise nutritional requirements of the pregnant ewe is still extremely limited, it is similarly impossible to describe the aim of such husbandry methods in any objective or definitive way. It cannot be stated, for example, what the intakes of digestible organic matter should be during pregnancy nor how these may be influenced by environmental factors. In general terms it can only be stated that the ewe should be well fed, particularly during the last third of pregnancy, that she should not be allowed to become overfat in early pregnancy, and that she must always be protected from sudden shortages of food, and from sudden environmental stress.

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CHAPTER SIXTEEN

Helminth Diseases of Grazing Animals

J. F. MICHEL AND C. B. OLLERENSHAW

Life cycles—Physical factors of the environment—Host resistance—Fluctuations in parasite populations—The design of control measures.

The helminth diseases of grazing animals are not only a major source of loss to the British livestock industry costing not less than ten million pounds per annum, but also represent an interesting and largely unexplored field of study for the ecologist. The subject is dealt with in this chapter from the point of view of population dynamics because that is the only possible way of dealing with it. If it is dealt with inadequately it is because as yet only a few workers regard the subject from this viewpoint.

The present account will attempt to suggest a few general principles of helminth epidemiology and to illustrate these in terms of the three outstandingly important helminth disease problems, parasitic bronchitis in cattle, fascioliasis in sheep and parasitic gastroenteritis in sheep, the last a complex of several parasitic diseases, due to varying combinations of some eight genera of strongyloid nematodes. The epidemiology of these three diseases presents an interesting range, fascioliasis and parasitic bronchitis being in many aspects at extremes with parasitic gastroenteritis occupying an intermediate position though only very little is yet known of single genera or species.

PARASITIC LIFE CYCLES

It may with some justice be argued that habits of thought are unduly influenced by the devices of pedagogy and this may be true of the

manner in which the life cycle of parasites is often represented Two life cycles depicted in this manner are shown in Figs 16 1 and 16 2 In the first are shown the various stages in the development of *Haemonchus contortus*, the large stomach worm of the sheep The male and female adult worms live attached to the wall of the fourth stomach and suck blood The females lay eggs which pass out in the dung The embryo in the egg develops and the first-stage larva hatches from the egg and feeds on coliform bacteria in the faeces After a time it

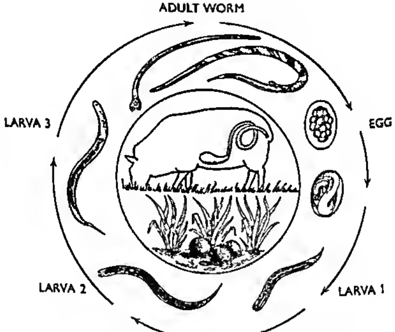

FIG 16 1 The life history of *Haemonchus contortus*

undergoes an ecdysis and, now dignified by the title of second-stage larva it continues to feed on coliform bacteria A second ecdysis takes it to the third stage but it retains the second skin, presumably with the sole object of tempting parasitologists to conclude that it does so to protect it from desiccation The larva is now infective It leaves the faeces and as some would have it, climbs into the herbage When swallowed by a sheep it completes its second ecdysis and burrows into the abomasal mucosa. It undergoes two more ecdyses before reaching the fifth or adult stage The life cycles of the other species concerned in parasitic gastroenteritis are very similar though *Bunostomum trigonocephalum* is capable of penetrating the host's skin Whether

this alternative mode of entry into the host is of great importance is however doubtful.

The life cycle of *Dictyocaulus viviparus*, the lungworm of cattle, is not greatly unlike that of *Haemonchus*. The adult worms are to be found in the smaller bronchioles. With their heads turned into the ciliary current they feed on the exudate which it brings to them. The females lay embryonated eggs which almost immediately hatch. The first-stage larvae are carried up to the mouth, swallowed and passed out in the faeces. The larvae do not feed and are sluggish in their movements. They pass through the normal three-developmental stages but never cast a skin so that the infective larva which may be recovered from the herbage coiled like a clock spring has no fewer than three cuticles which, however, appear to afford it only little more protection than the single skin of the first-stage larva. When the infective larva is swallowed by a calf it casts its outer skins, penetrates into the intestinal wall and finds it way into the lacteals. It is carried to the mesenteric lymph glands and passes into the venous blood through the thoracic duct. The first capillary bed that it meets is in the lungs and penetrating into the finest bronchioles it undergoes two further ecdyses before reaching the imaginal stage. The worms are mature some 21 days after infection. The time taken for the migration to the lungs has been the subject of some controversy. In the case of *Dictyocaulus filaria* in sheep it has been adequately demonstrated that the larvae develop to the fourth stage in the mesenteric lymph glands and then migrate to the lungs about the eighth day. Recent data published by Poynter *et al.* (1960) suggest that *D. viviparus* on the other hand migrates to the lungs about the second day while still in the third stage.

The life cycle of *Fasciola hepatica* is shown in Fig. 16.2. The adult fluke lives in the bile ducts, and produces eggs which pass out with the faeces. Given suitable conditions the egg develops into a free-swimming larva termed a miracidium which penetrates into a snail; in Britain the snail intermediate host is *Lymnaea truncatula*. There the miracidium develops into a sporocyst which in time gives rise to rediae. Rediae produce cercariae either directly or indirectly by means of daughter rediae. The cercaria is another free-swimming form, it leaves the snail and encysts on the herbage, the metacercaria thus formed surrounds itself with a tough protective coat, and entrance into the final host is achieved when the herbage is eaten. The cyst wall is digested in the intestine of the final host, the metacercaria

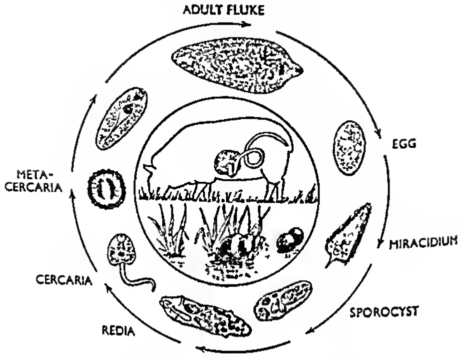

FIG 16 2 The life history of *Fasciola hepatica*

emerges, penetrates the wall of the intestine and eventually enters the liver. There the young fluke grows, enters a bile duct and reaches maturity some 10–12 weeks after ingestion of the metacercaria.

It will be seen that, in all of these life histories, the process of population increase takes place in more than one environment. The parasites cannot increase in number in the host nor can they increase in the outside world. Only if conditions in both or in all three environments are favourable and the parasite can succeed in passing from one environment to the next is an increase in population possible. The admirable circularity of these diagrams tends to obscure this extremely important circumstance that the passage from one stage to the next is attended by deadly hazards and is not just a matter of following the arrow.

Most parasites are extremely prolific. A careful calculation concerning the reproductive capacity of *Haemonchus contortus* has been made and its results are illuminating. If it be postulated that one male *Haemonchus* and one female *Haemonchus* on one thousand acres of pasture find conditions sufficiently favourable that they may reproduce at their normal rate, if none of their progeny dies prematurely and the life cycle is completed in five weeks, the adult worm living for a month,

then at the end of seven months the rate of increase of the worms would be such that a layer of worms on the thousand acres would be increasing in thickness at such a rate that the top of it would be moving upward at a speed equal to the velocity of light. It may be concluded that the reproductive potential of *H. contortus* is not reached under normal conditions of husbandry.

A heavy mortality is the necessary corollary of a high reproductive rate and the study of helminth epidemiology is chiefly a study of the causes of that mortality. The life cycle of a parasite might therefore be drawn as shown in Figs. 16.3 and 16.4. The life cycle is divisible into processes or phases of two kinds: development in a particular environment and transport from one environment to another. In each of these phases different causes of mortality operate. Reproduction is limited to the parasitic stage of the life cycle and the population at any subsequent stage depends on mortality up to that point. Populations of the non-reproducing stages of the parasite can decrease but not increase and are not subject to population pressure, to competition for food or to predators to the same extent as are completely free-

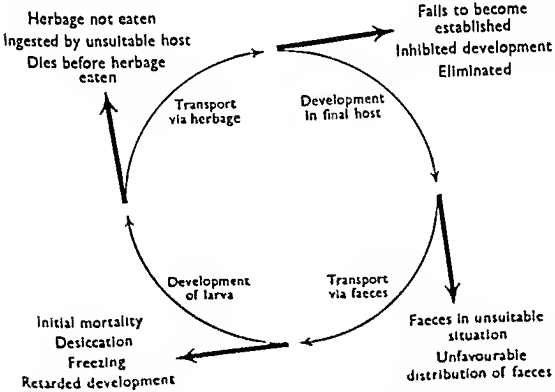

Fig. 16.3. A diagrammatic representation of the life cycle of *Dictyocaulus viviparus.*

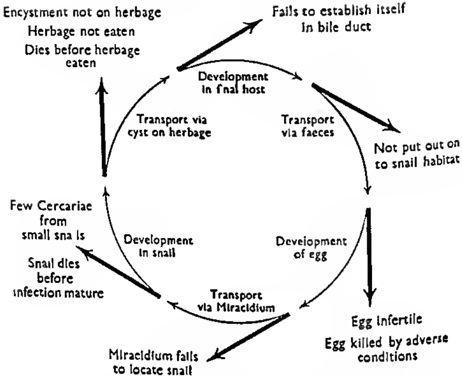

FIG 16 4 A diagrammatic representation of the life cycle of *Fasciola hepatica*

living species In consequence it is the effect of physical factors on mortality that dominates the dynamics of populations of the free-living stages

PHYSICAL FACTORS OF THE ENVIRONMENT

It is difficult and may be misleading to consider different physical factors and their effect on parasite populations singly for they are interrelated Yet in a discussion such as this it is inevitable It is axiomatic that the factors of greatest importance to the ecologist are those which in their action on the organism are the most variable The physical factors which largely concern the helminth epidemiologist are climatic The free living forms under consideration, however are not directly exposed to the effects of the climate Free-living existence starts in the faeces of the final host The microclimate within the faeces differs from that surrounding the faeces This the microclimate amongst the herbage is in turn not identical with that of the air above The herbage may be visualized as acting as a buffer between conditions in

the air and those in the soil. The extent to which the microclimate amongst the herbage differs from the macroclimate depends on the nature and state of the herbage. If the herbage is dense and tall it will be more effective in reducing or retarding variation in humidity, temperature or light intensity than if it is thin or short. Wind may, however, be an important factor in destroying the microclimate. The volume of the faecal aggregate determines its effect in reducing the effect on the parasite of changes in the microclimate among the herbage. For example a pat of cow faeces will offer much greater resistance to desiccation or temperature changes than will a thin smear of diarrhoeic faeces or a sheep pellet.

In normal conditions in Britain two factors, temperature and moisture, are of outstanding importance. The responses of different species of parasite to temperature vary. In the case of all there is a range within which temperature and rate of development are directly related. Both above and below this range there are regions in which there is no development but the parasite is not killed. Beyond these limits death results. Differences occur as between different species in the limits, especially the lower limits, of these ranges and the importance of temperature in the case of a particular parasite depends on the 'ecological temperature zero' of its development, i.e. the highest temperature at which development cannot be completed. In some cases as, for example, that of *Fasciola hepatica* it is sufficiently high to prevent development in most winters. In others as *D. viviparus* it is so low that development is possible throughout the year. To retard development, however, in a dwindling population will of necessity decrease the number which succeed in completing that development. This is discussed further in another section.

None of the free-living stages of the parasites with which this chapter is concerned is completely resistant to desiccation, indeed some are highly susceptible. Moreover, fluctuations in humidity are liable to be more violent and irregular than are fluctuations of temperature which tend to show regular cyclical annual and diurnal variations. The effect of humidity is important also on the movement of larvae out of the faeces. The faecal environment is a temporary one. Either the larvae actively migrate from the faeces or the faeces themselves disintegrate.

Much attention has been directed to the question of how the infective stages get on to the herbage. True it is that unless they come to be situated on the herbage they will not be ingested by the final host, bu

this circumstance has led to the assumption that all infective larvae climb into the herbage and that this activity is directed by toxis It is gradually becoming evident, however, that not all larvae are active and it is contended by some workers that random movement will adequately account for the conduct of those that are The term 'migration' now used in this connection may in time be replaced by 'nomadism'

HOST RESISTANCE

During its development and reproduction in the final host the parasite may also be subject to considerable environmental resistance due primarily to the defensive mechanisms of the host Sheep do not appear to develop any resistance to *Fasciola hepatica* infections, but host resistance plays an important part in the epidemiology of nematode infection.

The phenomena of host resistance to nematode infestation do not at first sight appear to conform to any pattern or system Especially is this so if, as is customary, resistance or immunity is regarded as a single entity It would seem, however, that a number of distinctions are useful Thus one may distinguish between acquired resistance, which is a consequence of infection and what might be called natural resistance, which may appear even in a host animal that has never had experience of infection. In this second category could be placed resistance due to age alone or to constitutional or nutritional causes Though age, nutrition and similar factors may also have an effect on the manifestations of acquired resistance the term natural resistance as used in this sense would not imply a defensive mechanism provoked by the parasite Sandground (1929) regarded age resistance as no more than a parasite finding that an old member of a sligbtly unsuitable host species was in deference to von Baer, more unsuitable than a young member

Acquired resistance also should not be regarded as a single entity A more useful approach is to visualize it as being composed of a number of separate manifestations which are only loosely or indirectly connected one with another Thus the infection may be terminated by the spontaneous elimination of adult worms, a mechanism termed 'self-cure' The phenomenon called 'inhibition of development' retards or suppresses entirely the growth and development of immature worms That known as protection' prevents newly acquired worms

from becoming established. Among other responses to infection which are also only indirectly related to each other or to the manifestations of acquired resistance are eosinophilia, the appearance of complement-fixing antibodies in the blood and local oedema though the last appears in some cases to be intimately connected with self-cure.

It is useful to regard these manifestations as separate and distinct for they differ not only in their effects but in their causation, rate of development and persistence so that an animal which is capable of one is not necessarily capable of another. It appears likely that these same manifestations of resistance are discernible in all associations between nematodes and mammals, but there are quantitative differences in the relative effectiveness of the various mechanisms in different host-parasite systems. These quantitative differences produce the appearance of qualitative difference and obscure the underlying common pattern. For example a local oedema may be seen either three weeks after first infection of a bovine with *D. viviparus* or twelve days after reinfection. In the case of *D. filaria* infections in sheep, however, a pulmonary oedema can only be produced as a result of a first infection (Michel, 1954). This difference is attributable to a difference in the effectiveness of the protection mechanism. In the reinfected calf sufficient larvae will reach the lungs to give rise to oedema. In the lamb with previous experience of *D. filaria* infection on the other hand, hardly any worms contrive to reach the lungs. The protection mechanism in *Dictyocaulus* infections in the calf would, however, seem to be much more powerful than that against *H. contortus* in the sheep. Thus reinfection with a massive dose will induce self-cure in an infection of *Haemonchus*; in an infestation of *D. viviparus*, protection and, in some measure, the inhibition of development make it extremely difficult to increase the mass of worms present and self-cure cannot be prematurely induced.

The phenomena of resistance play a singularly important part in the epidemiology of parasitic diseases for they determine both the limitations to the parasite's development and reproduction in the host and also the status of the host animal as a source of pasture contamination.

The protection mechanism exerts a profound influence on the pattern of population increase. Broadly speaking, one may distinguish between two such patterns. If the time required for the development of the protection mechanism is shorter than the minimum period in which the life cycle can be completed, then a sustained build-up of population

as between the pasture and the host will not be possible, the host being refractory to infection by the time it is contributing to the herbage infestation The worm burdens in the host will depend therefore on the level of the herbage infestation to which the host was exposed when its protection mechanism was still in a poor state of development The epidemiology of parasitic diseases in which this relationship obtains will be characterized therefore by sudden exposure to heavy herbage infestation and the infection process will take place over a short space of time

If the minimum period required for the completion of the life cycle is appreciably shorter than that required for the development of protection, the host animal will be able to reinfect itself and the worm burden ultimately resulting will depend not so much on the herbage infestation to which the animals were first exposed as the extent to which, over a fairly long period of time, the eggs or larvae passed in the faeces succeed in becoming infective forms on the herbage.

The times required to develop protection on the one hand and to complete the life cycle on the other are not fixed Both may in certain circumstances be affected by environmental factors Thus, to quote just two examples, the development of protection may in some instances be retarded or accelerated by the nutrition of the host animal, while the rate of development of the free-living stages may vary very widely according to the temperature Moreover, the two rates are interrelated since the development of protection depends on the rate of uptake of larvae from the pasture These relationships may be expected to modify the two basic patterns of population increase which have been outlined.

The characteristics of the host as a source of pasture contamination may also be regarded as broadly conforming to one of two patterns In the first of these protection develops rapidly and is effective, and the spontaneous termination of the initial infection leaves little or no residue. The output of infection in the faeces will therefore be short-lived and animals which have thrown off the infection will be only an intermittent source of pasture contamination. The second pattern is seen where the infection is not abruptly terminated by self-cure or where a substantial residue remains and reinfection or a large reserve of inhibited forms will ensure that there will always be some adult worms present. In consequence every animal which has experienced infection is a constant source of contamination.

FLUCTUATIONS IN PARASITE POPULATION

The operation of environmental factors throughout the life cycle of the parasite will tend to produce an annual rhythm in population fluctuations, for both climate and the pattern of livestock husbandry show seasonal changes. Winter temperatures are often too low for the development of the free-living stages. Summer may be too dry for their survival. Susceptible animals enter the flock or herd once a year, lambs being born at a particular season and calves housed during the winter and turned out to grass in the spring. Nutritional and physiological changes also follow a seasonal pattern.

Superimposed on a basic seasonal periodicity in parasite populations are sudden fluctuations of an interesting kind. It has been shown that the great majority of free-living individuals perish. It has also been shown how this mortality is greatly influenced by environmental factors. This situation of a normally high environmental resistance resulting in the survival of only one individual in thousands must imply that a relatively small decrease in environmental resistance will very greatly increase the effective population. For example, if in normal circumstances, 9,999 in every 10,000 individuals perish, then if the environmental resistance decreases so that the mortality is reduced by only one-tenth, 8,999 individuals out of every 10,000 will perish and the residual effective population will be one thousand times as great as normal. The effect of an increase in environmental resistance is not so spectacular for, if in our hypothetical example, we were to double the normal mortality we should only halve the number of survivors. It is clear that a small decrease in environmental resistance may result in a very great parasite population. Moreover, such conditions need operate only over a short period of time, a period of the same order as the normal duration of the parasites' free-living development.

If changes in worm populations are the outcome of the interaction of a seasonal periodicity and haphazard increases due to decreases in the environmental resistance, then it would seem to follow that a high population in any given year will not be attributable to gradually increasing populations in previous years nor will it influence the level of the population in subsequent years. All the evidence tends to confirm this conclusion.

THE DESIGN OF CONTROL MEASURES

It will be clear from the account that appears in succeeding chapters of the three major helminth diseases that a complete understanding of their epidemiology has not yet been achieved. A number of general comments appear warranted, however, regarding the elaboration and eventual application of control measures.

Thus it is necessary to distinguish between measures aimed at eradication and those aimed at control. It has been shown in an earlier section that parasites suffer a very high mortality at every stage of their life cycle and that in consequence great increases in population may result from a small decrease in environmental resistance. It is the function of control measures to stabilize that high mortality and to prevent those population increases which are the cause of disease.

That eradication measures, inadequately carried through, constitute a form of control is common fallacy based no doubt on the view that the control of parasitism consists of 'breaking the life cycle' at some convenient point. A complete break, were it possible, would lead to eradication. A break which was not complete would not necessarily affect parasite populations. For example, a reduction in numbers of an intermediate host would be effective only if the density of the intermediate host were indeed a limiting factor in determining parasite populations. Again measures designed merely to reduce the opportunity of an animal to reinfect itself via the pasture would have an effect only if outbreaks were the consequence of such reinfection. If, however, the development or persistence of an acquired resistance depended on contact with reinfection then such measures might increase the risk of disease.

Most environmental factors exert some effect, directly or indirectly, on more than one process or phase of a parasite's life cycle and this effect is rarely the same on all. It cannot be justifiable, therefore, to make deductions or devise control measures on the basis of an understanding of the bionomics of a single phase or stage. Such deductions inevitably contain far-reaching assumptions concerning the rest of the life cycle. Accordingly deductions regarding possible control measures must be based on an adequate understanding not only of all the processes involved in the life cycle but also of the manner in which these processes are related one to another. The whole is very much more than the sum of its parts and epidemiological research must be concerned not only with component parts of the life cycle studied in isolation but

also with experimental situations in which the parasite can complete its life cycle. In consequence helminthological experimentation must be conducted at a number of levels involving successively greater portions of the life cycle and in which successively fewer factors are regulated. Before the results of purely helminthological experiments can be applied in the form of practicable control measures, trials conducted in an agricultural context, their results assessed by means of agricultural criteria, are essential.

If deductions regarding control measures cannot be based on only a single phase or process considered out of relation to the remainder, so also is it impossible to make recommendations regarding isolated factors, conditions or practices which are 'favourable' or 'harmful to parasites'. Control measures must be part of a properly integrated system of practices associated with a simple policy and not a heterogeneous collection of inadequately defined beliefs. Since a number of alternative policies may be possible which may use entirely different methods, one perhaps aiming at controlled exposure to infection while another aims at complete freedom from infection, it is essential that a single policy must be followed and its basis clearly understood by all concerned.

It is to be foreseen that when control policies can be formulated the need for this detailed understanding on the part of those managing stock will be an important limitation to their effective application. At present it seems improbable that the complexities of helminth epidemiology can be reduced to simple slogans.

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CHAPTER SEVENTEEN

Parasitic Bronchitis

J F MICHEL AND C B OLLERENSHAW

Bionomics of free-living stages—Grazing behaviour—Translation—Survival—The parasitic stages—Acquired resistance—Population studies—Husk in adult cattle—Control

BIONOMICS OF FREE-LIVING STAGES

It will be evident from the discussion outlined above that the basis for the peculiarities of the epidemiology of parasitic bronchitis must be sought in the detailed phenomena of the bionomics of the larvae and of host resistance

Perhaps the two outstanding qualities of the free-living stages are their inactivity and their propensity for dying These circumstances were reported by Michel and Rose (1954) who showed that there was always a very great initial mortality, up to 98 per cent perishing in the faecal pat within a fortnight The rate of mortality tended to decrease and the declining larval population followed a smooth exponential curve, no apparent change in the rate of mortality being associated with different developmental stages Apart from the heavy initial mortality the larvae are highly susceptible to desiccation and first, second and third stages are equal in this regard As shown by Rose (1956), however, the different stages *do* differ in their reaction to freezing the third stage being somewhat more resistant The critical temperature for development is surprisingly low and development will take place slowly even in winter When at a temperature of 25° C development to the infective stage takes three days, it may require twenty-six days at 5° C

The larvae, then, tend to dwindle rapidly. They develop at almost every season and there is no resistant stage in which the larvae can persist during unfavourable times. The inactivity of the larvae and their failure to migrate from the faecal pat are striking. Michel and Rose (1954) showed that no more than one-half per cent or fewer of the larvae present succeeded in migrating from the undisturbed faecal pat and on to the herbage and in nearly every case all of these were less than five centimetres from the pat. In such a situation the larvae is unlikely to be picked up by grazing cattle and indeed the only possible suggestion, namely that in order to become infected cattle must ingest bovine faeces, raises some difficulties. Experiments on the grazing behaviour of cattle in relation to faeces show, however, that it is only when the faeces are in the form of obvious pats that they are reliably avoided by grazing cattle. Small particles of faeces or thin smears on the herbage appear not to be so readily recognized.

The effect of factors tending to spread the faeces over the herbage has been studied by Rose and Michel (1957) who concluded that the consistency of the faeces are of considerable importance, diarrhoeic faeces contaminating a much larger area than those of a normal consistency. Mechanical agencies such as mowers, harrows and the feet of cattle are also very effective in disseminating faeces, but it is evident that larvae widely spread in these various ways are more susceptible to desiccation, freezing and the like than larvae in faecal pats. Undisturbed faecal pats can in fact serve as a reservoir of infection which can be made available at a later stage by mechanical means provided that climatic conditions have left the pats in such a state that they can be spread.

GRAZING BEHAVIOUR

It is clear that it would be incorrect to think of larvae available to the grazing animal as larvae on the herbage. The larvae are in the faeces and the faeces are on the herbage and one must distinguish between deposits of faeces which are liable to be ingested and those which are not liable to be ingested. Experiments described by Michel (1955*a*) showed that grazing cattle consistently picked up fewer larvae than were present in random herbage samples taken by a standard procedure and that even when the samples were taken with the deliberate intention of avoiding what appeared to be contaminated herbage, they still contained a greater concentration of larvae than the herbage selected by the calf.

More recent data have shown that even random herbage samples do not provide an absolute measure of the level of infestation on the herbage. Sampling herbage and unrecognizable faeces implies a subjective judgement on the part of the observer and it appears that differences in the state of the herbage will have an effect on the process of herbage sampling more marked than its effect on the selectivity of grazing. Moreover, the extent of the process whereby larvae in the faeces become larvae on the herbage appears to influence the relationship between the numbers of larvae picked up by the observer in random samples and by the grazing calf, the observer picking up relatively more larvae in his random samples when larvae in faeces have been successful in becoming larvae on herbage. Variation in this relationship is not unduly great and a tolerable correlation may be shown between assessments of the concentration of larvae on the herbage and the infestation acquired by a calf. The dependence of the fate of a calf on the herbage count which it first encounters will be further discussed below.

TRANSLATION

An understanding of factors leading to the creation of high herbage infestations is essential to a knowledge of the epidemiology of lungworm disease. It has been shown in a variety of ways that the relationship between the numbers of larvae being passed on to the pasture in the faeces of infected animals and the resulting herbage infestations is extremely variable (Michel and Parfitt, 1955) so much so that the process whereby larvae in faeces become infective larvae on herbage, for which the term 'translation' has been used (Spedding and Michel, 1957), is regarded as of paramount importance. Indeed it may be said that the actual number of larvae being passed on to the pasture plays a relatively unimportant part in determining the level of infestation.

Various means of measuring this process have been used for purposes of comparison and there is evidence to suggest that its magnitude is related to the rate of herbage growth. The complex trains of causation involved in the effect of the climate on the process of translation are shown in Fig. 17.1. In order to become infective larvae on the herbage, the larvae in the faeces must be mechanically carried on to the herbage, they must develop and they must survive. The rate of growth of the herbage influences not only the consistency of the faeces

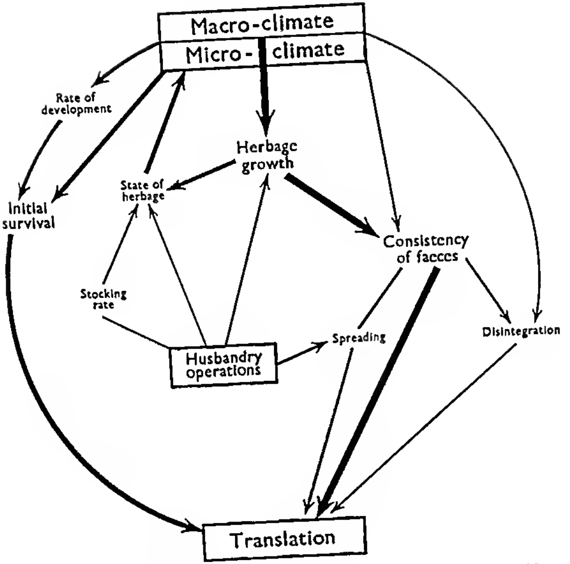

FIG. 17.1. Trains of causation in the effect of climate on Translation. (From Michel and Parfitt, 1956, *Vet. Rec.*, 68, 704.)

and thus the extent to which they will be spread but also the micro-climate amongst the herbage which greatly affects the initial survival. The rate of development, determined by the temperature has a considerable bearing on the numbers reaching the infective stage since the larvae die off at a handsome pace and any extension of the developmental period will decrease the number of infective larvae resulting. This is illustrated in Fig. 17.2. In very cold weather an extended developmental period would have the added effect of leaving the larvae for a longer period at a stage more susceptible to freezing.

Robinson (1962) has made an interesting contribution towards the explanation of the phenomenon of translation of the larvae of *Dictyocaulus viviparus*. In routine cultures of lung worm larvae he observed

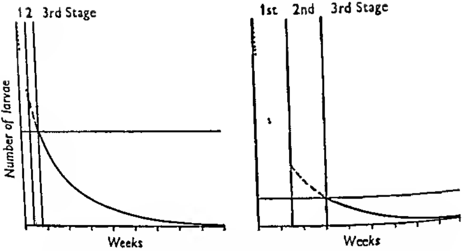

FIG 17 2 The effect of an extended developmental period on the numbers of *D viviparus* larvae reaching the infective stage

the development of sporangiophores of the phycomycete fungus *Pilobus* on the surface of bovine faeces A characteristic of *Pilobus* is the violent discharge of the ripe sporangium which may travel up to ten feet He noted that larvae migrated to the upper surface of the sporangium and were carried on discharge an appreciable distance from the faeces In a single experiment carried out in the field, active larvae were recovered from vessels placed at distances of up to ten feet from the faecal pat

Robinson points out that if this association is widespread, it must represent a significant factor in the epidemiology of parasitic bronchitis and the results of his extended investigations are awaited with interest

SURVIVAL

Conditions favourable for translation are not always similarly suitable for survival Nor are good conditions for survival necessarily suitable for translation In early summer, for example, very high herbage infestations may arise from small numbers of larvae in faeces but these high herbage infestations are unlikely to persist In winter the creation of high herbage infestations is extremely unlikely but existing herbage infestations generally survive well. Fig 17 3 is an idealized representation of the herbage larval count on a hypothetical paddock on to which the same number of larvae are passed every day in the faeces of calves grazing on it.

The period of survival of the larvae on a pasture is clearly not easy to determine. The general pattern of decrease implies that any definition of the survival period must be coupled with the criterion of presence or absence to be employed. With the passage of time the number of larvae present will decrease, the rate of decrease becoming ever less. An answer to the question, how long will lungworm larvae live on the pasture, will therefore depend entirely on the context and depend on the significance of very small numbers. The survival period is, of course, also largely influenced by climatic conditions, being shorter in dry conditions than in moist. It may be said that a pasture which has

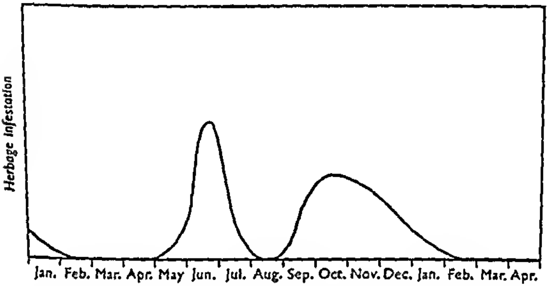

FIG. 17.3. Fluctuations in the level of herbage infestation on a hypothetical paddock on to which equal numbers of *D. viviparus* larvae are passed every day in the faeces of infected cattle.

been free of cattle for two months in summer or for four or five months in winter is unlikely to be carrying a dangerous infestation. Similarly after three or four summer months or after six to eight months the numbers of larvae it might be carrying will be so small as to be of no significance unless very unusual methods of husbandry are adopted. Normally, of course, herbage infestations disappear more rapidly than this and one should think of the appearance of lungworm larvae on the pasture as a transient phenomenon.

It would be wrong therefore to think of the pasture as a great and constant reservoir of infection or as the source of lungworm infection. It is far more useful to think of grassland as the vehicle by means of which infection is transmitted from one animal to another.

THE PARASITIC STAGES

A typical infection of *D viviparus* is short lived It is spontaneously terminated fifty or sixty days after infection by the elimination of the adult worms and thereafter the animal will resist reinfection to the extent that if it is reinfected the new worms do not grow to maturity and no larvae will be passed in the faeces All animals that have been exposed to infection are not, therefore, from that time onward a constant source of infection However, immature forms inhibited in their development will not be eliminated when the infection is terminated and may subsequently develop slowly, so also may the small numbers of larvae that may succeed in becoming established in the resistant animal exposed to reinfection Moreover, animals which encounter light infection—that is, not sufficiently heavy to cause disease—may carry small numbers of worms for considerable periods Thus, although all older cattle are not a constant source of contamination, they are liable to be an intermittent source and the importance of the carrier animal can hardly be overemphasized Carrier animals, discussed first by Wetzel (1948) and later by Michel and Shand (1955), Michel (1955*b*) and Michel and MacKenzie (1956), became the subject of a study of material from a knackery in the west of Scotland by Jarrett *et al* (1955) and Cunningham *et al* (1956) who found that an appreciable proportion of cattle were harbouring lungworms even after spending the winter in conditions precluding the possibility of reinfection Animals that had enjoyed only one grazing season were the most likely to be acting as carriers especially if they had not been clinically affected

Certain it is that the parasite may survive on a farm at a low level for many years without ever giving rise to recognizable disease Though farms entirely free of the parasite do appear to occur they are extremely rare and it is best to assume that the worms are present on every farm where cattle are kept. One may indeed divide farms into two categories from the point of view of lungworm infection On some, clinical husk occurs every year in cattle in their first grazing season. On others clinical husk occurs only rarely but may affect any age group This circumstance would suggest that animals which have experienced the infection become resistant. It suggests also that age alone does not produce a resistance to the parasite Both these conclusions have been confirmed and amplified by laboratory experiments It appears that both young and old animals are

equally susceptible to first infection with *Dictyocaulus* and a similar dose of larvae per unit of the host's body weight will kill a two-year-old beast in just the same time as a young calf. It does not follow from this, however, that the reaction of young and old animals to *Dictyocaulus* infection is identical in all respects.

As yet there is no direct evidence that constitution or state of nutrition affects resistance to lungworms and it appears that they certainly do not influence the establishment of a first infection. There are indications, however, that infections in older animals or in those in good bodily condition may be terminated more rapidly. Such animals also appear more liable to develop pulmonary oedema and emphysema as a result of lungworm infection.

ACQUIRED RESISTANCE

Acquired resistance has been the subject of considerable study and it appears that the protection mechanism is its most noteworthy manifestation. Only very small numbers of larvae become established in the lungs of animals that have recovered from the disease (Michel, 1955*b*, 1956*a*; Rubin and Lucker, 1956). The fate of larvae which fail to become established in the resistant host is still not entirely clear. Michel (1956*b*) working with *D. filaria* showed that equal numbers of worms are recoverable from the intestines and mesenteric lymph glands of resistant and susceptible mice while only few can be recovered from the lungs of the resistant mice. Similar results were obtained in rabbits and in lambs infected with *D. filaria*. It was shown that the number in the mesenteric lymph glands of susceptible lambs decreased while those in the lungs increased. Meanwhile, there was no increase in the numbers of worms in the lungs of resistant lambs. Further experiments, however, showed that the question is not necessarily just one of larvae being destroyed in the lymphatic system for if this is by-passed by the intravenous administration to sheep of exsheathed infective larvae, these also fail to become established in resistant though not in susceptible lambs.

In the case of *Dictyocaulus viviparus* where the migration to the lungs takes place earlier it has been shown by Poynter *et al.* (1960) that equal numbers of larvae can be shown to reach the lungs of susceptible and resistant calves and it is probably in the lungs of the resistant calf that the larvae are destroyed.

Much evidence is accumulating to show that it is the immature

stages of the parasite that are responsible for eliciting protective immunity From experiments with *D filaria* in which worms were transplanted from one lamb to another at different stages and in which the infection was terminated at different times with the aid of anthelmintics it appeared that the part of the infection that was essential to protection lay between the 10th and the 17th day. In the case of *D viviparus* also it is an early stage of the infection that produces resistance to reinfection This is the basis underlying interesting developments due to Jarrett and co-workers. It had been shown by several workers that nematode larvae could be attenuated by means of X-rays and that such attenuated larvae, though infective, would fail to complete their parasitic development. Gould *et al* (1955) showed that animals which had been infected with irradiated larvae of *Trichinella spiralis* were subsequently resistant to reinfection.

This principle Jarrett *et al* (1958, 1959, 1960) applied to *D viviparus* and found that it was possible to select a dose of X-rays which would permit the development of virtually no adult worms when irradiated larvae were administered to calves but which rendered the calves resistant to reinfection. Jarrett *et al* assumed that their irradiated larvae perished in the mesenteric lymph glands and that this was the site of antibody formation They held that the presence of dead larvae in the lymph glands was particularly effective in producing resistance

It has since been shown by Poynter *et al* (1960) that irradiated larvae are just as successful as normal larvae in reaching the lungs and that it is in the lungs that they perish. Jarrett *et al* found that a single large dose of irradiated larvae gave a good measure of protection but that two small doses not only gave rise to much less significant symptoms in the calves but also produced a more useful measure of resistance. This work resulted in the development of a husk vaccine which is now widely used

The protection mechanism develops fairly rapidly when a calf is infected Fig 17 4 shows the development of protection in calves which received on day 0 a dose of infective larvae sufficient to produce fairly severe disease The development of protection does not appear to depend in any way on whether self-cure has occurred Clearly it would be wrong to think of an animal as becoming resistant, throwing off its infection and thereafter being refractory to reinfection

The inhibition of development in *Dictyocaulus* infection has been discussed by Taylor and Michel (1953) and Michel (1955*b*) The onset of this mechanism is rapid. Indeed, even when only a single dose

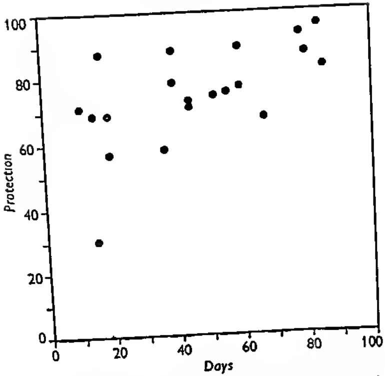

FIG. 17.4. The development of protection in animals receiving on day 0 a dose of 3500 larvae of *D. viviparus*. Protection is expressed as

$$T = \left(\frac{\text{worms established in resistant animal}}{\text{worms established in susceptible control}}\right).$$

of larvae is administered to a susceptible calf, a few, perhaps the last to arrive in the lungs, fail to grow at the normal rate. These are not eliminated when the infection is spontaneously terminated and may persist in the lungs for considerable periods of time. In consequence any animal that has been exposed to infection should be regarded as a potential source of contamination though the number of worms it may carry are small.

Pulmonary oedema which is associated with the extreme symptoms of parasitic bronchitis might also, with some justification, be regarded as a manifestation of acquired resistance. In experimental infections (Michel, 1954) pulmonary oedema and emphysema, the fog fever syndrome as it is called, tended to appear three weeks after a first infection or twelve days after the administration of a large dose of larvae to an animal that had had previous experience of infection. In some cases it appeared about the time of or a little after the spontaneous termination of the first infection.

Two syndromes occur in parasitic bronchitis but it would appear that it is not possible rigidly to distinguish between typical husk as seen in the calf and atypical husk as seen in adults. Coughing may be

regarded as a symptom of mild husk and dyspnoea associated with pulmonary oedema and emphysema, the fog fever syndrome, is a symptom of severe husk but both syndromes may occur in calves and in adults and a single individual may exhibit both during the course of the disease

It has been shown by Jarrett *et al* (1955) and by Weber (1958) that antibodies can be demonstrated in the blood of calves infected with lungworms by means of the complement fixation test using an antigen prepared from adult worms. Jarrett and his colleagues demonstrated, moreover, that a passive immunity could be produced in calves by the intraperitoneal administration of gamma-globulin prepared from blood rich in these complement-fixing antibodies which they therefore assumed to be protective It has since turned out, however (Michel and Cornwell, 1959) that the results of the complement fixation test using an adult worm antigen show no correlation with protection as measured helminthologically It must be concluded that antibodies which will combine with antigens made from the tissues of adult worms are not protective In a large trial of the immunizing properties of such antigens Jarrett *et al* (1960) confirmed this view producing only a very slight resistance

Recent successes in the *in vitro* cultivation of the parasitic stages of nematodes (Weinstein and Jones, 1956, Silverman, 1959) may justify the hope of imminent progress in the immunology of lungworm infection The possibility of producing in quantity not only the early parasitic stages but also their metabolic products should provide antigens not only for use in serological tests but perhaps also as vaccines

POPULATION STUDIES

Of the various manifestations of resistance it is the protection mechanism which dominates the epidemiology of parasitic bronchitis. The dependence of the fate of a calf on the herbage infestation to which it is first exposed was demonstrated by Michel and Parfitt (1956) They lightly infected a small paddock with lungworms and introduced a fresh susceptible calf every five weeks No living calf was removed except on one or two occasions when the paddock became grossly overstocked. The fluctuations in the herbage infestation closely followed the idealized course shown in Fig 17 3 in a manner bearing only a limited relation to the numbers of larvae being passed on to the paddock in faeces The fate of the calves, however, was closely

related to the level of herbage infestation at the time that each calf was first put out on to the paddock. Careful calculations showed that the best correlation was between the period of survival of the calf and the mean herbage count over the first nine days. In Fig. 17.5 the period of survival has been plotted against the initial herbage infestation for each calf. It will be seen that if the initial level was less than one larva per pound the calf survived no matter how high the level rose subsequently. It would clearly be an unsatisfactory explanation of this

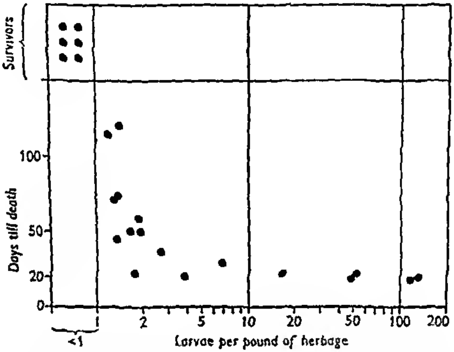

FIG. 17.5. The relationship between the period of survival of a susceptible calf and the herbage infestation to which it was first exposed. *'Initial herbage infestation' is calculated as the mean count over the first nine days.* (From Michel and Parfitt, 1956, *Vet. Rec.*, 68, 706.)

phenomenon to suggest that a calf becomes entirely refractory to infections of any magnitude in nine days from its first experience of infection. The uptake of larvae which a calf will tolerate at any given moment is related to the uptake which it has experienced up to that time. If the calf has been picking up larvae at a small rate, for a given number of days it will withstand a certain small rate of uptake. If it has been picking up larvae at a greater rate, what it will stand will be correspondingly greater.

With each successive day the proportion of the worms picked up which become established becomes smaller and one may visualize a

maximum rate of acceleration of the increase in the uptake of larvae or in the herbage infestation which the calf can stand Now in an experimental situation such as that under discussion the herbage infestation at any given moment is related to the herbage infestation on previous days What a calf has picked up and what it is about to pick up are therefore related in the same way as are what it has experienced and what it is capable of withstanding The experimental situation had a further peculiarity which contributed to the results obtained This was that the herbage infestation was low only when the potential rate of its increase was also low

One might expect therefore that it is only within a certain range of circumstances that the conclusion is applicable that a calf cannot build up on the pasture a herbage infestation which will be dangerous to it. However working under quite different conditions Michel and Mac Kenzie (1956) also came to this conclusion They exposed cattle varying in age from six months to two years to natural infection under conditions of set stocking and rotational grazing and demonstrated that the infections produced in the experimental cattle were due entirely to larvae which they had picked up over a short space of time and were in no part referable to larvae which they themselves had passed

Outbreaks of disease are not always the consequence of exposing susceptible calves to herbage infestations created by other cattle In situations in which increases in the rate of uptake of larvae are unduly rapid the same relationship between the initial herbage infestation and the fate of the calf may not apply

This was illustrated in an experiment in which two calves were given a very light infection of lungworms by the administration of a single dose of larvae and were then put on a clean pasture Conditions for translation happened to be good and a high infestation resulted on the herbage when they began to pass larvae This higher herbage infestation the calves could not resist and both quickly succumbed In this case on their clean pasture the calves picked up no larvae until a few days after their infection became patent and the rate of uptake of larvae to which they are suddenly exposed bore no relation to what they had experienced up to that time Similar happenings have also been seen with calves which were given a rather larger dose of larvae and were then put on clean pastures

In another experiment two uninfected calves were put on a clean paddock and infection was introduced ro this lungworm free system in a more natural manner when workers attending to the calves walked

first on an infected paddock before entering the clean paddock. After some weeks extremely small numbers of larvae began to appear in the faeces of the calves and a herbage infestation arose considerably higher than the minimum lethal level. The calves however, remained unharmed and were subsequently shown to be resistant to herbage infestation some twenty times the lethal level.

Clinical husk can also occur if calves are put on a very lightly infected pasture where conditions for translation are exceptionally good and the small numbers of larvae that they pass produce a heavy herbage infestation with undue speed.

The situations which have been discussed illustrate the general thesis that disease can occur only when animals with an inadequate protection mechanism are suddenly exposed to high herbage infestations. In the case of the experiments discussed above the calves were unable to resist the higher herbage infestation to which they were suddenly exposed because their previous experience of infection had not been adequate.

HUSK IN ADULT CATTLE

It appears that, in the absence of reinfection, protection tends to wane and cattle which have been withheld from contact with the parasite may not be able to prevent the establishment of worms in their lungs if they suddenly suffer a heavy uptake. Outbreaks in adult cattle are generally of this type. Only very few outbreaks in adults are the consequence of the introduction of infection into a worm-free herd. Such herds are extremely rare, but in the majority of cases the history of adult outbreaks suggests that the cattle have experienced a negligible uptake of worm larvae for some time and have then been suddenly exposed to heavy infestation. Very frequently individual animals which have for some reason or another been housed until a few weeks before the onset of symptoms are the worst affected.

A curious feature of many outbreaks of this type is the absence of larvae from the faeces of the affected animals. Often also no worms can be seen in the lungs of animals that die. This circumstance greatly complicates the confirmation of a diagnosis which normally depends on the demonstration of larvae in the faeces. The explanation is to be found in the phenomena of resistance for although protection wanes the other manifestations remain unimpaired. The worms reaching the lungs will give rise to a local oedema but they will fail to develop and most will be eliminated. Thus, although symptoms of disease

will appear, no more than a few immature worms may be recoverable at post-mortem examination.

An outbreak of this kind in cattle which had had previous experience of infection was recently produced experimentally (Michel and Coates, 1958) Cattle were exposed to moderate infection and then withheld from further contact with the parasite by strip grazing over clean ground and subsequently by yarding. A year after their first contact with infection they were again put on a moderately infected pasture together with fully susceptible control animals of the same age. Symptoms of equal severity appeared in both groups but while larvae appeared in the faeces of the control animals they remained absent from those of the previously infected cattle

This situation in which cattle are withheld from infection and then suddenly exposed to heavy herbage infestations may occur in a number of ways Many practices which are employed in the interests of better grassland utilization are effective also, in some measure, in denying the cattle access to larvae which they have passed in their faeces As we have seen, the numbers of larvae passed in their faeces by animals that have thrown off a mild infection will not be great nor will their output be continuous Animals which have been housed during the winter will not have encountered the worms and strip grazing during the first two or three months of the grazing season, over ground which has carried no cattle since the previous autumn and subsequently over aftermaths, may continue this freedom from contact. A frequent finding on farms where outbreaks of husk have occurred in adult cattle is that the cows and the young stock are kept on entirely separate pastures and even dry cows do not graze together with the young stock.

The small numbers of larvae passed in the faeces of carrier animals may give rise to dangerous herbage infestations in two ways If conditions for translation are particularly favourable, such high herbage infestations may be produced directly Alternatively, susceptible young stock exposed to the small herbage infestations produced by carrier animals will become lightly infected and the greatly increased numbers of larvae reaching the ground in their faeces will produce dangerous infestations The young stock may not be affected, however, by these high infestations which they themselves have created. It is therefore not possible to deduce that a pasture is clean from the circumstance that susceptible cattle have grazed on it with safety.

The occurrence of mild husk may be permissible in this context for recent work suggests that calves which are clinically affected and suffer a loss of weight may, under conditions of reasonable management, make up this loss. This is illustrated in Fig 17 6 which shows the weights of an infected group of cattle and of uninfected control animals. It is, however, extremely difficult to ensure a sufficient exposure to infection under farming conditions without a certain risk that it will prove excessive.

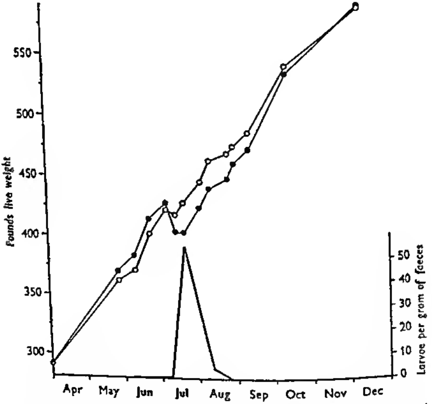

FIG 17 6 Mean live weights of husk infected cattle and uninfected control animals. Mean faecal larval counts of the infected group are also shown

The measures to be adopted to prevent serious disease must depen on the hazards peculiar to the district and to the particular farm. I some case it will be sufficient to segregate the yearlings, the group mo likely to be an active source of pasture contamination, or to avoi practices that must be regarded as particularly dangerous. Of the one of the most common is to turn out the strongest calves first an after a period of weeks, to add a second and sometimes even a thi

batch to them. In these circumstances the earlier calves can build up an appreciable herbage infestation to which the later calves are then suddenly exposed while fully susceptible. Another dangerous practice commonly encountered is that of turning out a few calves born in early summer during the autumn and then running these calves in the following year with autumn- and winter-born calves when they are first turned out in the following spring.

There has been some progress recently in the field of chemotherapy and two new anthelmintics have come into use. The action of cyanacethydrazide was reported by Walley (1957) who showed that this material acted as a vermifuge, temporarily paralysing the adult worms which were then swept up the trachea. The investigations of a considerable number of other workers into the action of this anthelmintic have produced a variety of results. Thus Swanson *et al.* (1959) could not show the drug to have any effect whatever on their experimental lungworm infections. Other workers were able to confirm the results of Walley while yet others, among them Rosenberger and Heeschen (1959), concluded that cyanacethydrazide was less effective in severely affected animals. This view appears to be widely accepted and accordingly Harrow (1959) has suggested that the material be used prophylactically, monthly doses being given throughout the summer in the hope that the calves will acquire infections sufficient to render them resistant but that the development of harmful worm burdens will be prevented. Since herbage infestations can arise very rapidly and outbreaks of husk are not the result of a slow build-up of infection in the calves and on the pasture, one would not expect monthly dosing with a partly effective anthelmintic to reduce the hazard very greatly. Indeed it has yet to be shown that such treatment is effective.

receiving the second dose This small dose of irradiated larvae gives rise to coughing or other symptoms only on infrequent occasions The resistance resulting from vaccination appears to be good, though it may prove insufficient if the animals are suddenly exposed to heavy infection Vaccination should not therefore be regarded as a substitute for all other precautions At the least, situations likely to be particularly dangerous should be avoided

It has been suggested that the adoption of a policy of vaccinating the calves will lead to the eradication of lungworm infection from the farm It would seem, however, that the vaccinated animal becomes entirely refractory to infection only when its resistance is reinforced as a result of exposure to infection Moreover, some individual animals appear incapable of a normal immune response Cornwell and Berry (1960) have shown that vaccinated animals can act as a source of infection It would appear probable, therefore, that while the general level of infection on a farm may be substantially reduced by a policy of vaccination, it is unlikely to disappear altogether If indeed lungworm infection falls to a low level then it may well be that the animal deprived of contact with infection may become susceptible and there may be the danger of an occasional outbreak in the adult stock

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CHAPTER EIGHTEEN

Parasitic Gastroenteritis

J. F. MICHEL AND C. B. OLLERENSHAW

Bionomics of free-living stages—Herbage infestation—Host resistance—Population studies—Nematodiriasis—The effect of husbandry practices—Control.

BIONOMICS OF FREE-LIVING STAGES

It is convenient if unimaginative to start an account of the epidemiology of parasitic gastritis with the worm egg. The rate of development of the embryo in the egg and its subsequent hatching depends on the environmental temperature. Under optimal conditions this process may be complete in twenty-four hours. The critical temperature for development and hatching of the egg does not appear to have been determined with precision for any species and although a figure of 65° C. for *Haemonchus contortus* given by Dinaburg (1944) is widely accepted it has been shown by Silverman and Campbell (1960) that development will proceed at temperatures considerably lower than this, although naturally at a slower rate. Thus, while development to the infective stage can be completed in a minimum of five days at 71° F., a minimum of 15 days is required at 51° F.; 50° F. is generally regarded as the critical temperature for the development of *Trichostrongylus* spp. and a critical temperature as low as 41° F. is attributed by Clunies Ross and Gordon (1936) to *Ostertagia* spp. Silverman and Campbell, however, suggest that *Trichostrongylus* and *Ostertagia*, while more resistant to cold and desiccation, develop more slowly at low temperatures than does *Haemonchus*.

The embryonated egg and the infective larva are more resistant to adverse environmental conditions than other developmental stages.

Indeed, development can stop at the pre-hatch stage if humidity or oxygen tension are too low and the embryonated egg may survive for long periods resuming its development when conditions improve If this stage has not been reached or if it has been passed when unfavourable conditions set in, then the egg or larva will die

As was intimated in an earlier section the free-living stages of a parasite are often insulated by virtue of their situation from fluctuations in climatic conditions, and the nature of the sward and the size and character of the faecal aggregate determine the extent of this insulation In much the same way the size and nature of the faecal pellet or faecal mass and the position of the worm egg in it will influence the rate of development In the centre of a pellet of faeces or in a larger mass of faeces, while humidity will remain high, the oxygen tension is liable to be low and this may result in the suppression of development at the embryonated egg stage Similarly, on the outside of the faecal pellet, oxygen will be plentiful but humidity may fall sufficiently to stop development As a result of the great range of conditions in which eggs will be situated and consequently of the different extent to which the development of different individuals is liable to be suspended, there will be a wide variation in the time taken to complete free-living development Although some individuals may become infective in the minimum time appropriate to the prevailing temperature, many will take appreciably longer, sometimes many times as long

Though the infective larva is more resistant than the first- and second-stage larva, it does not survive indefinitely on the pasture The results of Taylor (1938*a*) showed that the rate of destruction of third-stage larvae on the herbage was rapid at first and thereafter gradually decreased Crofton (1948*a*) was able to confirm this with the reservation that in cool moist conditions the rate of decrease may be less and remain fairly constant Clearly the persistence of larvae on the pasture depends not on a normal life-span but on environmental factors

Under dry conditions the great majority of the larvae may have perished in four weeks but in cold weather survival up to six months is not uncommon and small numbers may persist for longer The maximum survival period of various species is the subject of an extensive literature recently reviewed by Kates (1950), but it is of importance in only a limited context

Most workers who have studied the survival of infective trichostrongylid larvae have deliberately excluded from their experimental

designs differences in the rate of development to the infective stage; they have worked with infective larvae produced beforehand in carefully tended faecal cultures. In the application of the results of such experiments to practical problems, however, this fact has not always been remembered. It has been assumed that even in the field the larvae will all develop as rapidly as they will under optimum conditions in the laboratory. Hence it has been calculated that populations of larvae will have declined to a harmlessly low level when in fact they have only had time to reach their peak.

The migration of the infective larvae on the herbage has also received much attention. The movement of the larvae up the grass blades has been viewed as a negative geotaxis, but it has been argued that the force of gravity acting on the larva is negligible, in comparison with the surface tension in the film of moisture in the leaf. The view now coming to be held is that the movement of the larvae is at random, Kauzal (1941) having shown that upward migration was invariably accompanied by downward migration. Lateral movement is limited presumably because the soil offers resistance to movement. The activity of larvae may, to some extent, be influenced by the intensity of light but it is temperature which exerts a decisive influence, migration being entirely suppressed at temperatures below 50° F.

It would appear that in England for an appreciable part of the year the temperature would be too low for infective larvae to leave the faeces and ascend into the herbage. Such a consideration, however, is of limited relevance since temperatures too low for the migration are also, with the possible exception of *Ostertagia*, too low for development. To this extent the results of experiments in which infective larvae suspended in water are pipetted on to the soil of experimental plots may be misleading.

The presence of a film of moisture appears to be essential for the movement of the larvae and determines the upper limit of migration. Thus Crofton (1948*b*) reports that under comparable conditions larvae ascend to within the same distance of the top of the grass blades irrespective of whether these are in a long or a short sward. The local humidity down amongst the herbage was sufficient to produce a surface film of moisture, but nearer the tips of the grass blades free moisture was absent.

There is very little evidence to support the view that there is a regular alternate movement of larvae up and down the herbage in response to changes in humidity or light intensity and the belief that

larvae migrate up the herbage when there is dew on the grass and down again into the soil when the dew dries is almost discredited. Indeed Crofton (1949) has shown that the concentration of larvae per pound of herbage is highest in the hottest part of the day and lowest when there is dew on the grass. Crofton appears to interpret this in terms of greater larval activity at higher temperatures, but it is difficult to see why decreased activity should lead to a smaller concentration of larvae. The phenomenon may in part be explained by the circumstance that a given quantity of herbage will be heavier when it is saturated with dew and it may be concluded that there is no daily rhythm of migration. It would be more useful and more accurate to think of the larvae as migrating at random when it is warm enough but, having got on to the herbage, showing no particular tendency to descend to the soil again.

HERBAGE INFESTATIONS

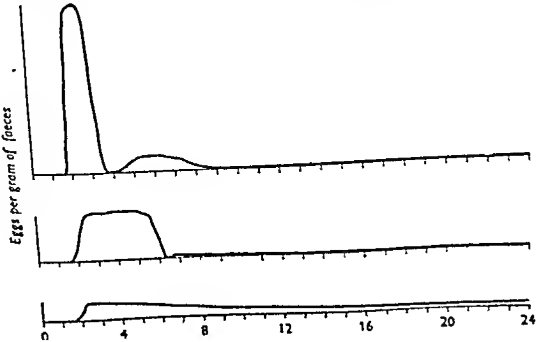
It is theoretically possible that sudden changes may occur in the availability of larvae on a pasture, when climatic conditions become suitable for migration. As has been shown, however, such a situation is unlikely to arise. An assessment of the infestation of a pasture by the examination of the herbage would seem therefore to be justified. As yet very few such measurements have been made with a view to following changes in the level of herbage infestation and those that have, have neither distinguished between the larvae of different species nor taken account of the number of worm eggs being passed on to the pasture in the faeces of grazing animals. There is therefore no experimental basis for a discussion of how the properties of the larvae and climatic and other factors interact to give rise to a seasonal pattern of herbage infestation. Such studies as have been reported suggest that there are no spectacular fluctuations in the infestation of the average sheep pasture nor do climatic factors appear to exert an overriding influence, for the peak in herbage infestation is reached at different times in the year on different fields (Crofton, 1952). The general pattern, if such can be said to have yet emerged, appears to be characterized by a low herbage infestation during the winter, rising gradually in the late spring and early summer to a peak from which there is a more or less rapid decline in late summer and autumn. Although there may be very considerable variation in the degree to which eggs in faeces become infective larvae in the herbage, it appears to be true

that seasonal fluctuations in herbage infestations are largely influenced by the seasonal pattern of egg output in the faeces of sheep. Before seasonal fluctuations in worm burdens can be discussed it will be necessary to consider the phenomena of host resistance.

HOST RESISTANCE

Among the trichostrongylidae relatively little work has been done on the phenomena of host resistance. The study of the manifestations of resistance as separate and only indirectly connected mechanisms has been pursued only in the case of experimental infections of *Trichostrongylus retortaeformis* in the rabbit. These observations, as yet inadequately reported (Michel, 1952*a*, 1952*b*, 1952*c*, and 1953), while not directly applicable to all species of trichostrongylus, may give indications as to the type of processes to be expected and also because they are nearer to a complete picture.

Infections of *T. retortaeformis* are, as a rule, relatively short-lived and their termination, which is by the elimination of adult worms, is fairly sudden. The duration of the infection bears an inverse relation to its size. This is shown in Fig. 18.1 which represents the course of three infections of different size as traced by faecal egg counts. When an



infestation too small to be abruptly terminated has superimposed upon it a second infection, the result depends on the size of the second infection This is indicated in Fig 18 2 which shows the course of a small infection and the consequence of reinfection with four different doses of larvae If the reinfecting dose is small the effect is purely additive and even the resulting larger infection is not abruptly terminated If the reinfecting dose is larger the faecal egg count first rises and the infection is then terminated If it is very large indeed, the infection is terminated in a week, before even the newly administered worms have reached maturity Some individual rabbits, however, fail to achieve self-cure As shown in Fig 18 3a their faecal egg counts rise sharply and they succumb It would appear from these facts that the termination of the infection is dependent on the quantity of worm material present and that there is no essential difference between the

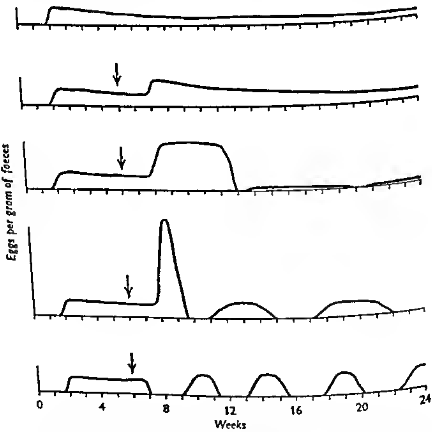


FIG 18.2 The effect on faecal egg counts of superimposing a second infection on one too small to evoke self cure

spontaneous termination of an infection resulting from a single administration of larvae and the termination of an infection induced or precipitated by reinfection, and the use of the single term *self-cure* would seem to be justified for both. This term was coined by Stoll (1929) in connection with the spontaneous termination of infections

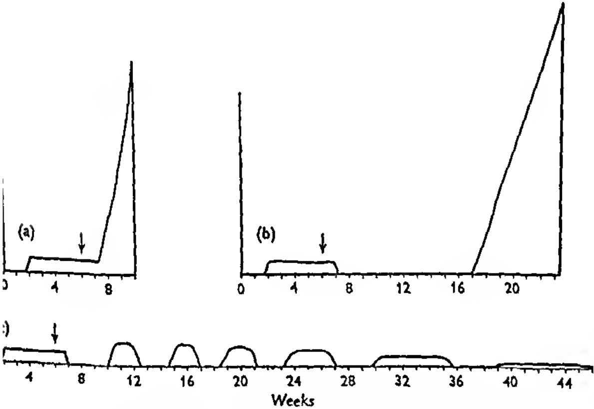


FIG. 18.3. The course of infections of *T. retortaeformis* after a large infection has been superimposed on a small one.

of *Haemonchus contortus*. Stoll lightly infected two lambs with *H. contortus* and turned them out on a paddock on which they reinfected themselves. Their faecal egg counts rose and after a few weeks abruptly fell almost to zero. This fall in faecal egg count Stoll called self-cure. Stoll now attempted to reinfect the lambs by the administration of large doses of larvae but they proved entirely refractory and this refractory phase Stoll termed 'protection'. This will be further discussed below.

The termination of an infection induced by reinfection was described by Gordon (1950) and by Stewart (1950*a*). These workers observed that infections of *Haemonchus contortus* as measured by faecal egg counts, in sheep grazing on arid pastures disappeared a few days after a shower of rain had stimulated a vigorous growth of grass. It transpired that

experimentally the same effect could be produced by the administration of a large dose of *Haemonchus* larvae and that the adult worms were eliminated, the newly administered worms became established and after three weeks the egg count began to rise again The Australian workers called this phenomenon self-cure and apparently restrict the term to just one form of it, that represented by the third graph in Fig 18 2

Considerable progress has been made by Stewart (1950*b*, *c*, 1953) in elucidating the nature of the self-cure process Thus it may be inhibited by antihistaminic substances, it is attended by an oedema of the stomach wall and followed by both a rise in blood histamine and of complement-fixing antibodies It is not entirely species-specific and the administration for example, of *H contortus* larvae may terminate an infection of *Trichostrongylus* spp though the administration of *Trichostrongylus* larvae will not terminate an infection of *Haemonchus*

The phenomenon of inhibited development has attracted attention in the case of several species If a rabbit carrying an infection of *T retortaeformis* is reinfected with a large dose of larvae, the majority of those established fail to develop and may remain in the late third stage for a period of months in close apposition to the mucous membrane. The development of these larvae is entirely suppressed, not retarded and once they resume their development, they proceed at the normal rate Normally the proportion of larvae resuming their development each day is fairly constant, but occasionally none appear to do so until a considerable time has elapsed whereupon all do and the animal succumbs The faecal egg counts of such a case are shown in Fig 18 3b The more usual course of such an infection is shown in Fig 18 3c. After the termination of the initial infection eggs remain absent from the faeces for a time and then after two weeks or so reappear as the first of the new worms reach maturity These worms are soon eliminated and after a further interval a further batch of worms which has resumed its development begins to reach maturity and eggs again appear in the faeces This sequence continues until no inhibited larvae remain. It may be concluded from evidence such as this that the self-cure phenomenon does not affect the inhibited late third-stage larvae and that it is elicited when the quantity of worms present reaches a certain threshold value The situation may be compared with a tank fitted with a syphon (Fig 18 4) A constant slow stream of water enters the tank and represents the resumption of development When the water in the tank representing quantity of worm material

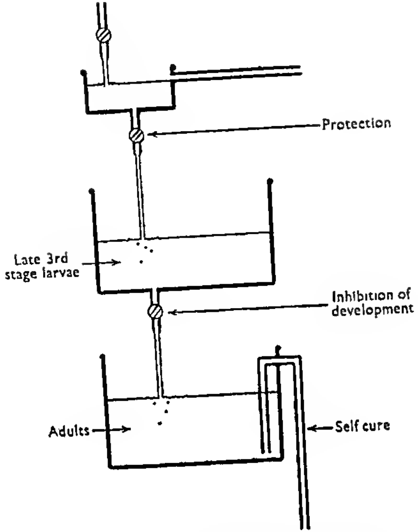


FIG. 18.4. A system of tanks which serves to illustrate the functioning of the manifestation of resistance to *T. retortaeformis*.

reaches a certain level, the syphon which represents the self-cure mechanism comes into operation and completely empties the tank.

A similar situation exists in infections of *Trichonema* spp. in the horse (Gibson, 1953). Here large numbers of worms may become encysted in the intestinal wall and their development inhibited over a period of years. When the adult worms present in the lumen of the intestine are removed by means of an anthelmintic their place will be taken by a similar number of worms which emerge from their cysts and resume their development. Even if horses are withheld from reinfection it therefore requires a great many treatments with an anthelmintic, spread over a long period, until all the inhibited forms have emerged from the mucosa, developed and been destroyed. In the case of *Haemonchus placei* in cattle the worms may be inhibited and will only resume their

development when the adult worms present are removed by means of an anthelmintic (Roberts 1956) The occurrence of the phenomenon of inhibited development has also been reported in infections of *Ostertagia* spp in sheep (Sommerville 1953) and there is evidence that it is of importance in *Ostertagia* in cattle though as yet little is known of the factors associated with the resumption of development in these species In *Trichostrongylus retortaeformis* infections the decrease in the numbers of inhibited forms drawn in Fig 18 5 tends to be more rapid than could be entirely accounted for by resumption of development and subsequent self-cure, but as yet there is no evidence concerning the fate of such larvae

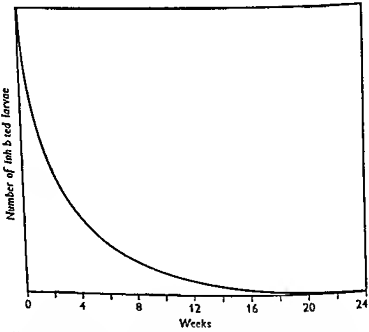


FIG 18 5 The decline in numbers of inhibited larvae in the absence of re infection

To demonstrate the phenomenon of protection in infections of *T retortaeformis* is difficult A rabbit which has received a single dose of larvae of any size is not at any time thereafter demonstrably more resistant to the establishment of a second dose of larvae than is a fully susceptible rabbit If however larvae are regularly administered to a rabbit then a resistance to the establishment of the new worms may be demonstrated Thus if rabbits are given increasing doses three times a week for three weeks and thereafter receive regular equal doses the

numbers of inhibited larvae present in the intestines of the rabbits will rise to a peak after six to eight weeks and thereafter decline again as shown in Fig. 18.6. Clearly newly-administered worms are failing to become established after six to eight weeks and the decline in inhibited forms after this point is similar to that obtained in the absence of reinfection (Fig. 18.5). Experiments in which dosing with larvae was discontinued just after the peak was reached in one of two groups but not in the other have shown that the decrease in population is very similar in the two groups, the slightly greater persistence observed in the animals in which reinfection was continued presumably being due to the small number of worms that were still succeeding in establishing themselves. In all other respects the course of the infection was identical in both groups and it would be true to say that everything happening in the constantly dosed rabbits was referable to larvae which they had received in the first six to eight weeks.

The number of adults of all sizes, that is to say of worms which have resumed their development, follows a course similar to that of the

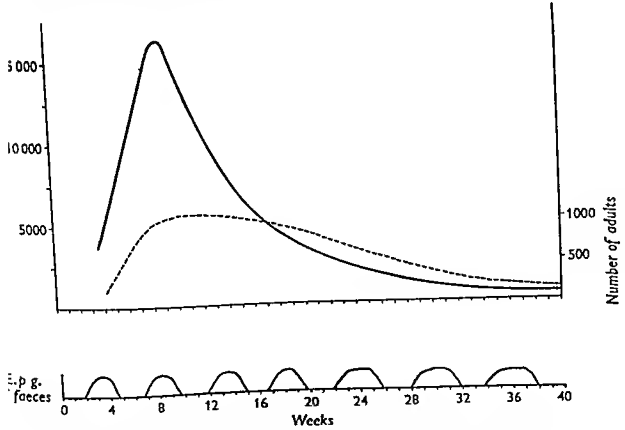


FIG. 18 6. The course of an infection of *T. retortaeformis* in rabbits receiving regular frequent doses of larvae. Above are shown the numbers of inhibited larvae and of adults of all sizes. Below are the faecal egg counts.

number of larvae but lagging behind it by a period roughly equal to the normal prepatent period This circumstance suggests that the larvae when they resume their development, grow at the normal rate and that the numbers which resume their development is related to the total number present The faecal egg counts meanwhile follow a familiar course, eggs intermittently appearing and disappearing from the faeces (Fig 18 6) At first sight this would seem hard to reconcile with the smooth curve marked 'adult worms' but these comprise all worms which are not inhibited third-stage larvae and indeed it is found that sometimes the worms recovered are mature and sometimes immature, sometimes even they are in the fourth or earliest fifth stage. It would follow that a population of worms in animals exposed to reinfection and even those withheld from reinfection, is by no means static Instead one group of worms follows another in rapid succession and though the number of adult worms may remain roughly constant for a considerable period it is not the same individual worms that are present throughout that period

The effect of a number of extraneous factors on resistance must also be considered It appears reasonably well established that nutrition of the host plays an important part Thus Gordon (1950) has shown that the duration of infections of *H contortus* and of *Trichostrongylus* is shorter in well fed sheep Gibson (1955) considers that well nourished sheep even if they have not had previous experience of infection are better able to prevent the establishment of *T axei* Stewart and Gordon (1953) on the other hand found nutrition to have little effect on either natural or acquired resistance to *Trichostrongylus colubriformis* Besides an effect on resistance to worms there seems also to be an effect of nutrition on resistance to the effects of worm infestation Constitution bodily condition and age are also regarded by some competent observers as exerting an influence on resistance to *Trichostrongylid* infestation and its effects

POPULATION STUDIES

In England only few studies have been made of seasonal changes in the worm burden of sheep Crofton (1955) followed the faecal egg counts of lambs on a number of farms and found that these rose to a peak in late summer and autumn and then decreased again usually fairly rapidly Crofton showed that the increase in egg count was logarithmic and from this drew a number of interesting conclusions

Thus a logarithmic increase would seem to imply that the worm burden of the lambs at any time is proportional to a previous infection or that it is related to the pasture contamination produced by the lambs. Such a situation Crofton argues, suggests among other alternatives that each new infection replaces a previous one, the rate of increase not being sufficiently great to render the old worm burden insignificant in comparison with the new. This is supported by a consideration of the individual counts of the lambs which tended to show an intermittent appearance and disappearance of worm eggs in the faeces, a smooth curve being obtained only by taking the mean count in a group. In other words, the successive disappearances of eggs from the faeces did not occur simultaneously in all the lambs and though they could be regarded as being in the nature of self-cure they must have differed in their causation from the self-cure described by Gordon.

The circumstances described by Crofton are not unlike the happenings which have been described as occurring in rabbits receiving regular doses of *T. retortaeformis* larvae (see Fig. 18.6). In this case, however, the faecal egg count is greater after each self-cure. After the protection mechanism appears, the faecal egg count declines as the inhibited larvae which resume their development decrease in numbers. A further implication of the logarithmic increase is that the infections in the lambs would seem to be dependent on the herbage infestation to which they were first exposed and, since residual infestation surviving through the winter is small, this initial herbage infestation would depend both on the faecal egg output of the ewes and on climatic conditions in the spring. It would appear also that the phenomena reported by Crofton and the arguments based upon them depend on a fairly constant relationship between the number of worm eggs being passed in the faeces and the number of larvae becoming available on the herbage, on a short period of development and on a short survival of the infective larvae on the pasture, a combination of circumstances that may not be of very frequent occurrence.

The seasonal incidence of stomach and intestinal worms in hill lambs in Scotland as studied by Morgan, Parnell and Rayski (1951) differs from that in lowland lambs in that the infections persist longer and may in fact not reach a maximum until the winter or the following spring and Morgan, Parnell and Rayski (1952) point out the connection between this and winter outbreaks among hoggs (yearling sheep) of black scour associated with heavy infestations of *Ostertagia* and *Trichostrongylus*. Perhaps the most significant finding of these authors

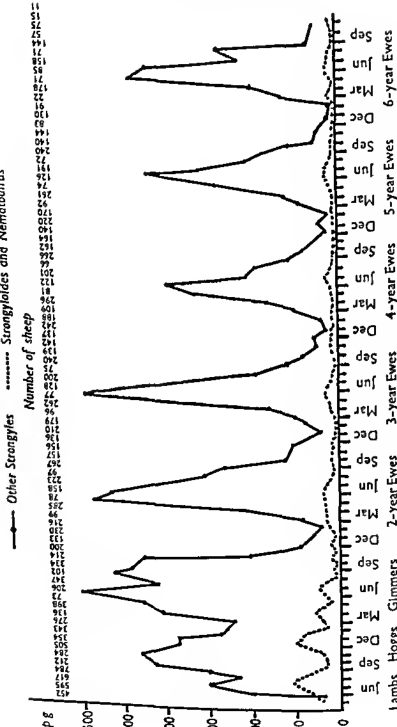


Fig 18 7 Seasonal variation in the variation of faecal egg counts of Scottish hill sheep (From Morgan Parnell and Rayski, 1951, J Helminth, 25, 177)

concerns the seasonal fluctuations in worm burden in adult sheep. At first this work was based entirely on egg counts and no effort was made to distinguish between different species save *Strongyloides* and *Nematodirus*, the eggs of which are very readily distinguishable from those of the other strongyles. The egg counts of ewes were shown to rise in the spring beginning in March, to rise to a peak in May or early June and then rapidly to fall (see Fig. 18.7). Moreover, it was shown that this pattern was common to ewes all over Scotland. The causes of this spring rise were the occasion of considerable discussion. If the rise was to be due to larvae picked up in the spring these would have had to be available in February which seems extremely unlikely. Three other possibilities were considered: that the spring rise was due to an increase in egg-laying by a constant number of females as a result of a decreased resistance in the ewes due to poor nutrition during the winter and the strain of lambing; that, for a similar reason, though no more larvae were picked up from the pasture, a larger proportion became established; and lastly, that the spring rise was due to immature worms which had lain latent through the winter and now grew to maturity.

To elucidate this question an extensive series of slaughterings and post-mortem examinations was undertaken. Some of the results of these are summarized in Fig. 18.8 which has been drawn from figures presented by Morgan, Parnell and Rayski (1951). It appeared that the rise in egg count was associated with an increase in adult worms and this in turn was preceded by the appearance of large numbers of immature forms in the lumen of the bowel. *Ostertagia* spp. were chiefly responsible for the rise and were followed by *Trichostrongylus* spp. Only very few inhibited immature forms could be found by the methods employed. True it is that *Ostertagia* is allegedly capable of developing at low temperatures, but there are, none the less, serious objections to the suggestion that the spring rise is occasioned by larvae picked up in late winter or early spring.

A spring rise in the worm-egg output of ewes has been observed not only throughout Scotland but by various workers in several different countries and there is no reason to suppose that all these reports do not refer to the same phenomenon. Now in the observations of several workers the spring rise occurred in sheep which had no access to infection during the appropriate period. Thus the sheep observed by Taylor (1935) were housed during February and March in conditions deliberately calculated to preclude the possibility of infection.

The sheep of Naerland (1949) in Norway and those of Hawkins *et al.* (1944) also showed a spring rise although they were housed throughout the winter. The sheep of Spedding and Brown (1956) showed a spring rise though they had been denied access to infection by being close-folded over clean land for some months. It may be concluded therefore that the spring rise is not necessarily associated with the uptake of larvae shortly before.

Crofton (1954) has added to knowledge of the spring rise by the interesting observation that the spring rise in individual ewes occurred at different times and was of much shorter duration than the curve given by a mean count of the whole flock. It appeared furthermore that there was a close relationship between the time of lambing and the appearance of the spring rise, the peak of egg count being reached some six to eight weeks after lambing. This is shown in Fig. 18.9. These results provided further evidence as to whether the spring rise was attributable to larvae picked up three or four weeks before, for even in ewes in lambing late when the herbage infestation must already have

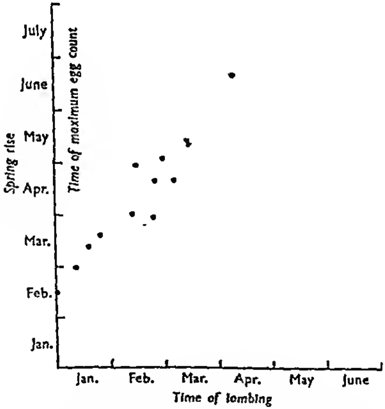


FIG. 18.9. The correlation between spring rise and the date of lambing. (From H. D. Crofton, 1954, *Parasitology*, 44, 465.)

been rising the faecal egg count rose no higher than in ewes lambing at the beginning of the season Crofton (1958) has since shown that a post parturient rise in faecal egg count occurs also in ewes lambing in autumn

Perhaps the most tempting interpretation of the spring rise would appear to be that lambing in some way interferes with the inhibition of development and that immature forms, primarily *Ostertagia* and *Trichostrongylus*, are able to develop to maturity The resulting increased worm burden is short-lived since it is sufficient to evoke self-cure It would not be unreasonable to conclude that the seasonal fluctuations in the worm burden of ewes are not to be associated with changes in the level of herbage infestation This state of affairs would seem to differ from Australian conditions where it has been found possible to make serious attempts to base control measures on changes in the weather

If the herbage infestation has normally little effect on the worm burden of ewes it appears that the egg output of the sheep on to the pasture has some influence on the herbage infestation

NEMATODIRIASIS

A recent renewal of interest in the epidemiology of *Nematodirus* spp is probably attributable both to the ineffectiveness of phenothiazine against this worm and to the circumstances that its eggs are very readily distinguishable from those of other trichostrongylidae Tetley (1941) working in New Zealand showed that the infection appeared in lambs in the spring and then rapidly disappeared being virtually absent until the following spring from animals of any age In England outbreaks appear to occur in lambs only during a very short season usually between the end of May and the beginning of July (Thomas and Stevens 1956 Thomas 1959)

It appears that the infection is carried on from lamb to lamb and year to year Thomas and Stevens found that on fields which had been grazed by infected lambs appreciable numbers of infective larvae did not appear on the herbage until the following spring The larvae develop to the third or infective stage before hatching from the egg and it appears that their development is very slow (Thomas and Stevens 1960 Gibson 1959*b*) especially in the case of *N battus* which may take three months to reach the infective stage The eggs even if development of the larvae is complete do not hatch until the following spring

usually not until the following April, the essential stimulus according to Thomas and Stevens (1960) being a rise in temperature to at least 50° F. after sensitization by exposure to low temperature during the winter. Thereafter there is a rapid decrease in the herbage infestation (Gibson, 1957).

Resistance to *Nematodirus* appears to be acquired rapidly and there is some evidence of the occurrence of a true age resistance (Gibson, 1957). The conclusion drawn by numerous workers is that lambs should not be allowed to graze on pastures which have carried lambs in the previous year, and Thomas and Stevens maintain that the study of the histories of many outbreaks amply confirms this view.

Progress has also been made in the field of chemotherapy. As reported by Rawes and Scarnell (1958) bephenium embonate is effective not only against adult *Nematodirus* but also against the immature stages which are responsible for much of the damage caused by *Nematodirus* infection. Since the period during which there is a hazard of nematodiriasis is short, Scarnell and Rawes (1959) have suggested that periodic dosing with bephenium compounds will serve as a prophylactic measure.

THE EFFECT OF HUSBANDRY PRACTICES

It is necessary to discuss in connection with the epidemiology of parasitic gastritis the effect of certain aspects of management. As has been intimated in an earlier section the processes and operations of husbandry affect helminth populations through a great many different trains of causation and the effect of a change in management will be the outcome of an antagonism between several operating in different directions. It is impossible therefore to deduce on theoretical grounds what the effect of a given system of management will be. This can be determined only by field experimentation conducted on an adequate scale. Very little such experimental work has been carried out and it appears that such as has been done in Britain has been concerned solely with confirming traditional knowledge on the effect of close-folding. A theoretical discussion of certain speculations which are accepted as items of parasitological dogma may, however, be of value.

Perhaps the most important and widely accepted concerns the effect of density of stocking on helminth infestations. Making a number of assumptions Taylor (1938*b*) has suggested that the infestation on the

pasture tends to increase as the square of the stocking density This would seem to be an understatement for, making the same assumptions it can be shown that the effect of density of stocking increases, being related with the passage of time to successively higher powers of the density The assumptions on which such calculations are based, however, are quite hypothetical and it is necessary in them to neglect such important factors as host resistance and the transitory nature of a herbage infestation In practice density of stocking cannot be divorced from other circumstances Under conditions of agriculture all the herbage will be utilized even if not in the most advantageous manner, and a higher density of stocking will be associated with a more productive pasture Thus under conditions both of light and heavy stocking a given number of larvae will be suspended in roughly the same weight of herbage and it matters little whether that weight of herbage is grown on a large or a small area However, the rate of growth of the herbage in the case of the heavier stocking density will be greater and each portion will tend to be grazed more frequently Within a certain range of conditions, therefore, there will be a tendency at a low density of stocking for larvae to be older and therefore fewer by the time they are ingested

At any given moment, on the heavily stocked area, since grazing will be heavier, there will often be less herbage per unit area. Now if a given number of larvae is to be suspended in a small quantity of herbage a high concentration will result On the other hand a short herbage will not provide favourable conditions for the survival of larvae which are more likely to be exposed to desiccation. Indeed this effect may outweigh that of lesser dilution unless the atmospheric humidity happens to be high. The effect of stocking density will therefore depend on climatic and other adventitious factors Among these may be the state of nutrition of the animals which, in some circumstances, may be worse as a result of heavy stocking and in others better

The effect on worm burdens of rotational grazing has also been widely discussed in theoretical terms, the thesis being that the herbage infestation is greatly reduced in the period between successive grazings However, as has been discussed in an earlier section, the rate of free-living development under the climatic conditions obtaining in Britain tends to be much less than has been commonly assumed so that the period of rest between successive grazings of the same paddock would need to be almost impossibly long

In discussing *Dictyocaulus viviparus* which develops more rapidly and with which the difference between the rate of development of the quickest and the slowest can be neglected, Michel and MacKenzie (1956) have suggested that the effect of rotational grazing also is the outcome of the interaction of antagonistic factors.

Under conditions both of set stocking and rotational grazing, given a constant output of worm eggs by the animals, the same total number of larvae will be deposited on to the pasture in the period in which rotationally grazed animals complete one circuit of their small enclosures. In the case of set stocking each portion of the pasture receives its quota of larvae not at once but spread over a period, and since the larvae begin to die almost at once, the herbage infestation can never be so high as under conditions of rotational grazing where each strip receives all its quota of infection within a few days. On the other hand, while under conditions of set stocking the animals are immediately exposed to the lower herbage infestation which results, they are not exposed to infection under conditions of rotational grazing until some time has elapsed and the higher herbage infestation initially created has fallen. The relative effects of these two systems of grazing management would seem to depend therefore on whether climatic and other factors were favourable for the creation of high herbage infestations or for their persistence.

Another thesis frequently discussed concerns the practice of mixed grazing. It is claimed that a contaminated pasture can be cleaned by allowing a different class of stock to graze it and so eat off the larvae. It is probable that the effect of this is greatly overrated. Grazing animals after all do no more than to eat herbage and with it such larvae as happen to be on it. What is of importance is not the total number of larvae on the pasture but the concentration per unit weight of herbage. Reducing the total weight of herbage does not of itself reduce the effect of this concentration, indeed since most of the larvae are found near the base of the grass blades it is more probable that the herbage removed contains a smaller concentration than that which is left and the infestation per unit weight of herbage on the pasture may actually be increased.

It is clear that mixed grazing as such has no particular virtue in reducing the risk of parasitism, but there can be little doubt that it represents a means of utilizing with safety, pastures which are being rested. It must be borne in mind, however, that a number of species are transmissible from cattle to sheep. Roberts (1942) succeeded in

transmitting a number of species from sheep to cattle, among them *H contortus*, *T colubriformis*, *T axei* and *C curticei*

A corollary to the thesis concerning mixed grazing claims that alternate grazing with resistant stock of the same species is also effective in reducing the risk of helminthiasis Now, as has been shown, resistant sheep represent a constant source of infection though it is certainly true that their faecal egg counts tend to be lower than those of lambs and hoggs Speculations on this subject have consequently taken the form of calculations designed to show that ewes ingest and destroy more larvae from the pasture than they themselves contribute to the herbage infestations The validity of these calculations tends to be restricted, however, to conditions which are unfavourable for the creation of high herbage infestations and in which outbreaks of parasitic gastroenteritis are unlikely to occur in any case Where conditions for translation are more favourable it can be shown that ewes would not decrease the berbage infestation and might in fact add to it. In practice the question of whether to practise alternate grazing with ewes and lambs would only arise after the lambs were weaned and it is doubtful whether at this stage the practice would be likely to have any effect on worm burdens

Any discussion of control measures must be preceded by a consideration of the effect of infection on productivity A number of investigators, among them Kates and Turner (1953) working with *Nematodirus spathiger* and Gibson (1955) studying *T axei* infections have shown that infections depress live-weight gain and that affected sheep, when they have thrown off the worms, though they may resume the normal growth rate will never catch up with uninfected control animals (Fig 18 10) Spedding (1952, 1953, 1955) has obtained similar results with subclinical infections of *T axei* and of mixed trichostrongylids, and Taylor (1954) on the basis of such figures has estimated the annual loss in terms of tons of mutton.

CONTROL

Control measures must have regard to accurate assessments of loss since the control of worms is normally undertaken for economic rather than aesthetic reasons and the cost of control measures must be less over a period of years than the loss which they prevent. This consideration would seem to apply particularly to the system of close-folding over clean land which has been recognized for a century or

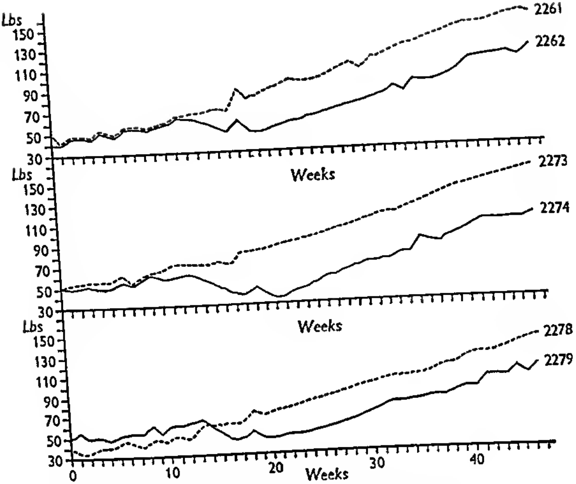


FIG 18 10 The effect of *T. axei* infection on the weight gains of lambs (From T. E. Gibson, 1955, *J. Comp. Path.*, 65, 317.)

more as preventing the transmission of worms. It may be that the procedure would be of use in the production of fat lambs on new leys and certain it is that if carefully carried out it is possible to rear lambs all but worm-free. The suggestion of Spedding (1954), however, that it is a means of achieving the complete eradication of worms from a flock and that such a worm-free flock could then be managed by normal methods so that the cost of close-folding for a year or two would be in the nature of a capital expenditure, should be regarded with caution.

Knowledge of the relationship between husbandry and helminthiasis is, it must be admitted, conspicuous by its paucity and this is in large part due to the discovery of the anthelmintic efficiency of phenothiazine, an efficiency so remarkable that its effect on research into the epidemiology of parasitic gastroenteritis was disastrous. That there are now signs of a slight recovery is due only to the gradual realization that even phenothiazine has limitations. That it is not equally

effective against all species has already been mentioned and recently Gordon (1950) has drawn attention to the difficulty of controlling an outbreak by dosing when very large numbers of immature worms are present which are unaffected by phenothiazine The view generally taken in Britain is that the most effective use of phenothiazine is as a prophylactic measure and that lambs should be dosed at monthly intervals throughout their first year Crofton (1955), however, has observed that regular dosing of lambs with phenothiazine reduced not only the rate of increase of the worm burden but also the rate of decrease

If regular monthly dosing is not found practicable it is generally recommended that one treatment should be given when the lambs are weaned Weaning is regarded as a time of particular danger on the grounds that the withdrawal of milk often coinciding with a deterioration in the quality of the pasture must adversely affect the resistance of the lamb Whether or not this deduction is sound, it is certainly true that outbreaks of parasitic gastritis in lambs not infrequently occur shortly after the lambs are weaned

Regular dosing of ewes is not generally regarded as necessary, but it has been suggested that since the spring rise is chiefly responsible for the herbage infestation in the spring to which the lambs are first exposed, anthelmintic treatment aimed at reducing the spring peak of egg output and thus the initial herbage infestation would be beneficial It should be stressed, however, that the degree to which eggs in faeces become infective larvae on the herbage is very variable and a reduction in the egg output of the ewes if it could be achieved would not alone be likely to be very effective in limiting the infection of the lambs

Considerable discussion has been devoted to how the practical difficulties of dosing hill ewes around lambing time may be overcome In some lowland flocks these difficulties should not be insuperable, but as yet there is no evidence from controlled experiments of the effect on the worm burden of lambs of dosing the ewes just before the occurrence of the spring rise

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CHAPTER NINETEEN

Fascioliasis

J. F. MICHEL AND C. B. OLLERENSHAW

Ecology of the intermediate host—Free-living stages—Development in the snail—The final host—Effect of climate: geographical distribution, climate and incidence of fluke.

ECOLOGY OF THE INTERMEDIATE HOST

Intermediate hosts tend to receive an undue share of attention, no doubt because they are frequently the only tangible part of the life cycle outside the final host which may be investigated. *Lymnaea truncatula*, the intermediate host of *Fasciola hepatica*, is no exception. The fact that it is essential for the continuance of the life cycle and that reproduction of the parasite occurs at this stage inevitably involves the snail in a vital and sometimes spectacular role, and as such deserves attention but no more than should that, for example, of the hatching of the fluke egg. An understanding of the ecology of the snail is however necessary in order to appreciate the precise relationship between the snail and the parasite.

L. truncatula is the only host of practical importance in Great Britain (Kendall, 1950). Its distribution can best be understood by first describing the moisture conditions which it requires. These are that the soil surface should be saturated with water together with a little free water on that surface and where the pH of the water is not too low for the survival of the snail. It is in areas where these conditions occur that the snail is found. These may be drainage ditches, muddy gateways, springheads, overflows from drinking troughs, heavily poached land, around broken drains, badly drained land, and flushes on the

hills (see Mozley, 1957). The snail is thus found (see Fig. 19.1) in areas where there is no rigid distinction between land and water, and because of this it follows that there are no sharply defined limits to the snail's distribution. Such areas are greatly influenced by the prevailing climate and may therefore vary from season to season, and year to year.

Obviously, in such areas the snail will be subjected to alternating periods of drought and wetness and the response of the snail to such changes is the dominating feature of its ecology. When there is sufficient moisture the snail is active, it grows, and eventually reproduces; when there is not, the snail aestivates (remains dormant) and in this condition can neither grow nor reproduce. Ideal moisture conditions throughout the year are rarely encountered in natural habitats, but from such cases it is possible to deduce the normal cycle of the snail which is shown in Fig. 19.2. *L. truncatula* is basically an annual having one generation in the year, egg-laying commencing in March or April, the daughter generation appearing in May. Reproduction of the parent snails continues into the summer during which time they die, so that by September the parent population has largely disappeared. The number of daughter snails reaches its peak about August. Growth of the daughter snails continues during autumn, but is largely arrested during the winter. There is, however, little mortality and the population is well maintained until March, when growth and breeding

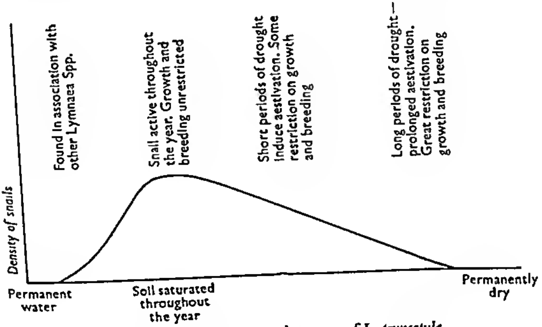

FIG. 19.1. The moisture requirements of *L. truncatula*.

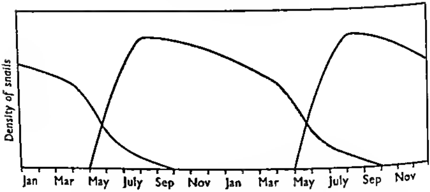

FIG 19 2 The normal breeding cycle of *L truncatula*

recommence but with increasing mortality, which continues throughout the breeding season

This basic cycle may be modified mainly by the intervention of dry conditions, but sometimes by other factors so that occasionally a second generation of daughter snails is produced in the autumn, parent snails may live through a second winter with or without breeding in their first spring, the breeding season may be split into two—spring and late summer by the intervention of a drought breeding in a very dry spring may not occur in which case the parent snails aestivate, often the parent population, having spent most of its life aestivating, may be represented by a few individuals capable of breeding, the same is true of very dense populations where the growth of individual snails is extremely slow

The precise effect of dry conditions on the snail may be seen by draining habitats This increases the environmental resistance and the snail responds by aestivating Young snails appear to withstand adverse conditions better than old snails Thus, if a habitat is drained in spring, the parent population undergoes a marked initial fall followed by a more gradual decline If the habitat is drained in summer, there is little mortality during that year but a considerable one the following spring followed again by a more gradual decline In either case, as is shown in Figs 19 3 and 19 4, even after a period covering two breeding seasons there still remains a small residue of snails Reduction of the environmental resistance in habitats that become wet, induces the snails to become active, and depending on the time of the year breeding follows Their response to favourable conditions is remarkable and increases of population from 10 to 800 per square metre in twelve weeks have been encountered

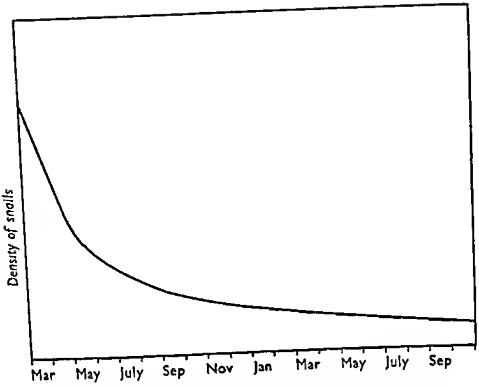

FIG. 19 3. The effect of drainage in spring on a population of *L. truncatula.*

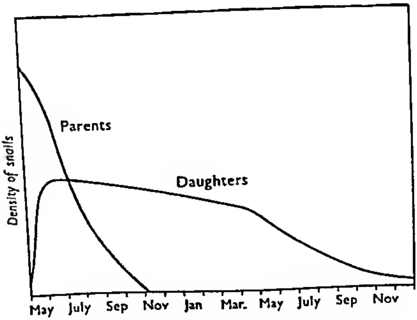

FIG 19 4. The effect of drainage in summer on a population of *L. truncatula.*

The snail is thus adapted to an ecological niche in which there are few competitors, and except for occasional birds, no predators, but where the hazards due to changes in climate are severe. Although drought substantially reduces snail populations, individual snails are able to survive for long periods and can quickly repopulate habitats with the return of suitable moisture conditions.

Although the snail is essential to the completion of the life cycle of the fluke, its degree of importance cannot be assumed. It is necessary to analyse the effect of snail populations on the level of fluke populations and to determine whether the snail plays a dominant role in the life cycle. Obviously the snail must be present for the cycle to be completed. This implies that the habitats of the intermediate and final host should overlap. That the final hosts do graze on areas which may be habitats cannot be denied, but such areas of pasture are not usually particularly attractive nor productive. Further, since the habitats of the snail are localized whilst the grazing area is not, the vast majority of eggs put out by the grazing animal irrespective of prevailing climatic conditions stand no chance of completing the cycle. However, when the population of snails is high and covering a wide area the chances of completion of the life cycle are greater and although it is usual to find a high snail population where there is an outbreak of disease, observation shows that it is not a necessary prerequisite to a high fluke population. This suggests that other parts of the life cycle are important.

FREE-LIVING STAGES

As yet little is known about the phases from the final host to the snail. There is little or no resistance to the fluke by the final host, and since a variety of animals may act as hosts it follows that in those areas where fascioliasis occurs there will be a daily output of eggs on to the pasture. Those eggs not deposited in habitats stand no chance of infecting a snail, whilst those eggs put on to habitats do not necessarily develop. Observations reported by Rowcliffe and Ollerenshaw (1960) show that, in order to hatch, the egg must become separated from faeces, there must be an adequate temperature for development, and sufficient moisture to prevent death from desiccation. The fact that there is almost no development below 10° C indicates that temperature is an important limiting factor for much of the year in Britain. Although eggs in moist faeces remain viable for long periods

at temperatures below 10° C. in winter, and could in theory lead to a mass hatch of miracidia in early summer this has not been detected to any noticeable extent.

Although there is a large daily output, the number of eggs that eventually succeed in hatching can never approach this number. In both the transport and developmental phases the egg may be subjected to great environmental resistance and unlike the snail has no great powers of adaptation so that fluctuations in numbers hatching are much more violent than changes in snail density and as a result are more likely to exert a greater effect on the ultimate fluke population. It should, however, be stressed that because there is daily output of eggs the fluke can respond to any lessening in the environmental resistance more quickly than the snail.

It is well known that the miracidium has a free life of about twenty-four hours during which time contact with a snail must be made. This obviously constitutes a great hazard and density of the intermediate host is likely to be an important factor, but there are indications that it is the number of fluke eggs hatching rather than snail density which determines the level of fluke infection. Even when a snail is contacted, penetration may not lead to infection (Roberts, 1950).

DEVELOPMENT IN THE SNAIL

It might be thought that in any habitat which had a population of snails approaching 3,300 per square metre all the fluke eggs hatching would succeed in infecting a snail and a very high infection on the herbage would result. However, in such cases the population pressure is such that this is not so. Infected snails in these conditions do not produce many cercariae and a high percentage die before the infection becomes patent. It is not therefore a simple case of many snails producing much fluke. Indeed the highest herbage counts have been recorded on habitats with quite moderate densities of snails (200–600 per sq. m.). In such cases the population pressure was quite small, the habitat not being restricted, with the result that all the snails were growing rapidly, those infected containing many large rediae and consequently producing large numbers of cercariae. There is no doubt that there is a precise relationship between the number of cercariae produced and the growth of the snail. Kendall (1949) studied nutritional factors affecting the development of *F. hepatica* in the snail in

the laboratory and Table 19 1 confirms his findings in natural populations

TABLE 19 1 *Relationship between size of snail and number of rediae (all mature infections)*

mm.	1 1–2	2 1–3 0	3 1–4 0	4 1 5 0	5 1–6 0	6 1–7 0	7 1–8 0	8 1–9 0	9 1 10·0
No of Rediae	8	13	17	34	44	55	68	81	103

Instances of high herbage counts and low snail densities (50–200 per sq m.) indicate that any estimate of fluke populations on the basis of snail densities may lead to erroneous conclusions Results obtained so far show that a density of 5 snails per square metre carrying mature infections existing under little environmental pressure is sufficient to produce a dangerous cyst count on the herbage In terms of snails this is an extremely low density and the fact that this density of infected snails can at times be achieved in snail populations of the order 50–200 per square metre would indicate a less prominent role for the snail in the life cycle

Not only is development of the fluke within the snail conditioned by the population pressure of the environment on the snail but it is also subject to the effect of physical factors The ecological temperature zero according to Kendall and McCullough (1957) is 10° C which, as with the egg, is high enough to be important Aestivation of the snail also affects the fluke as has been demonstrated by Kendall (1949) Development is restricted but the fluke survives as long as the snail, and development proceeds normally once the snail becomes active Again the dominant feature of development of the fluke in the snail is its interaction with the climate

The production of cercariae from infected snails does not inescapably follow Infected snails are diseased snails and this may be seen in laboratory cultures where mortality among infected snails is often severe The production of cercariae from snails carrying a mature infection is inhibited at temperatures below 9° C and the actual mechanism of production is obscure (Kendall and McCullough, 1957) but experiments show that it can be initiated by a slight fall in temperature Since cercariae encyst on a variety of objects there must be a further wastage of cercariae at this stage, but once the cercaria has

encysted, the remainder of the transport phase is passive and depends on the grazing of the final host. The metacercaria surrounded by its protective coat is in a resistant phase so that it is not essential for it to be eaten by the final host immediately. Various assessments of the duration of viability of the cyst on the herbage have been made (see Olsen, 1947). Our experiments, as yet incomplete, indicate that survival during winter is to be measured in months, and during the height of the summer in weeks. Detachment of cysts from the herbage appears not to occur to any appreciable extent provided the herbage remains alive.

THE FINAL HOST

As already indicated habitats do not usually provide particularly palatable grazing for stock, but, towards the end of the grazing season, pastures whether grazed by cattle or sheep tend to be eaten bare. This problem is intensified during winter in the case of most sheep pastures and this circumstance is likely to be of importance in view of the small size of habitats compared with the total acreage available. It seems relevant at this stage also to mention the emphasis that has hitherto been placed on the fact that *L. truncatula* is a mud snail. Granted that the snail can most easily be seen where there are patches of bare mud, but it has been found just as frequently in habitats where there was a complete cover of vegetation and indeed it should not be forgotten that the presence of herbage is an indispensable factor in the life cycle. The accidental ingestion of snails with mature infections, and the drinking of cercariae play no part in the infection of the final host since it is only after some hours of encystment that metacercariae become infective.

Cyst counts on the herbage are not particularly meaningful, but perhaps it is of interest to record that in habitats where fluke is causing trouble, counts in the region of about 1,000 cysts per lb. (2,200 cysts per kg.) of dried herbage are obtained. These cysts may of course be eaten by a variety of final hosts, but in this country only three are of importance: sheep, cattle and rabbits. Cattle have some measure of resistance and seemingly are not as much affected as sheep whilst until recently little attention has been paid to rabbits. There is no doubt that the rabbit is an important host; in some habitats they have been responsible for up to 90 per cent of the fluke eggs being put out.

The infection in sheep may take one of two forms. The chronic

form is due to a long-standing infection of a few flukes, and the acute form is due to large numbers of immature flukes migrating through the liver at one time

EFFECT OF THE CLIMATE

A feature of outbreaks of acute fascioliasis is their wide occurrence on many farms in an area, irrespective of the rates of stocking, differing husbandry practices and routine precautions It is the uniformity of such outbreaks which confirms that physical factors of the environment are most important Those such as the topography of the land and its geological structure which may affect drainage, or the soil type which may or may not retain moisture, play a part in determining the severity of an outbreak but it is temperature and moisture that are all-important

Tables 19 2 and 19 3 show the effect of temperature on the development of the fluke egg (see Rowcliffe and Ollerenshaw, 1960) and on maturation of cercariae within the snail together with the mean monthly temperatures for several stations

TABLE 19 2 *Effect of temperature on fluke egg development*

Temperature °C	°F	Incubation period of fluke egg (days)	Maturation of cercariae (days)
10	50	No development	No development
15	59	40	63
20	68	20	34
25	77	12	26

It will be seen that development is limited for varying periods during the year principally during the latter part of autumn, winter, and early spring Observations still in progress indicate that during summer, development from deposition of the fluke egg to maturation of cercariae takes at least 11 weeks Temperature, however, shows regular cyclical changes so that its effect will be broadly similar in different years, and variations in the level of fluke populations from year to year cannot be directly attributed to it.

Undoubtedly moisture is the most important single factor Snail habitats because of their very nature will provide suitable conditions

TABLE 19.3. *Monthly averages of mean temperature (1921–50) to nearest °C.*

Station	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov	Dec.
Balmoral, Aberdeen-shire	1	2	3	5	9	11	13	12	10	7	3	2
Bellingham, Northum-berland	2	2	4	6	9	12	14	13	11	8	4	3
Holyhead, Anglesey	6	6	7	8	11	13	15	15	14	11	9	7
Newquay, Cornwall	7	6	7	9	11	14	16	16	15	12	9	7

for development of the fluke when the surrounding land is at field capacity. Usually soil attains field capacity in the autumn, maintains this level through the winter, and loses it sometime in spring. In summer it is usually below field capacity. Thus the effects of temperature and moisture are in the main antagonistic, temperature suitable in summer, moisture in winter. Rainfall, however, varies greatly and in wet summers both factors are in unison. It is the variation in moisture during the summer which influences the level of fluke population.

Of itself, rainfall does not give a measure of field capacity, but some estimate of it may be made by determining the difference between rainfall and evaporation. The former may be measured, whilst the latter can be calculated (*Tech. Bull. No. 4*, Ministry of Agriculture, 1954). Obviously if evaporation exceeds rainfall the land is going to dry out and conditions will be unsuitable for the development of the parasite; if rainfall exceeds evaporation the land will remain at field capacity. The level of fluke populations will therefore be related to the length of time that rainfall exceeds evaporation during that period when temperature does not limit development. As has been seen it takes approximately three months of continuous development from the deposition of the fluke egg to maturation of the cercaria so that the maintenance of an excess of rainfall over evaporation for such periods will be important, though some development is to be expected even when the 'wet'* periods are not continuous.

* 'Wet' indicating that rainfall exceeds evaporation.

GEOGRAPHICAL DISTRIBUTION

Rainfall and evaporation data are usually calculated on the basis of calendar months Obviously a number of permutations are possible and indeed do occur, and when related to temperature they go some way in explaining both the geographical distribution and the varying incidence of fascioliasis in Britain From the data it can be seen that temperature is, on the whole, not limiting during the period May to October Consequently it is variation in soil moisture during these months which is of importance Examination of rainfall and evaporation data for differing parts of Britain reveals three distinct patterns According to the first, seen in the counties of eastern England, evaporation normally exceeds rainfall throughout the months of May, June July and August Obviously in such areas unsuitable moisture conditions exist most of the time that temperature is not limiting so that very little disease is encountered

The second pattern is characterized by an excess of rainfall over evaporation all the year These conditions lead to peat formation the acidity of which is inimical to the snail, which is not found widely distributed in such areas This pattern is found mainly in the hills and mountains of Britain under conditions of high rainfall and low temperatures In these areas the snail does occur but in small localized habitats termed flushes green patches of herbage surrounding springheads Moisture conditions in such habitats remain relatively uniform, but often the temperature is too low for development to be completed in one season so that the parasite overwinters in the snail and emerges on to the herbage in the following summer The combination of these factors with that of the long life of the hill ewe result in constant but low fluke infections in hill flocks in this country, severe epidemics of acute fascioliasis being rarely encountered Table 19 4 shows the results of sampling such a flock for fluke eggs in November

TABLE 19 4 *Incidence of fluke eggs in hill sheep in November*

Age of sheep (years)	Lambs	1	2	3	4
% infected	9	18	35	79	72

The third pattern is between these two extremes, occasionally all the months are 'wet', occasionally all the months are 'dry'*, but more often some are 'wet' and some 'dry'. September and October are almost invariably 'wet', so that the greatest variation occurs in the months of May, June, July and August. It is in areas with this third pattern that fascioliasis can be expected, and the varying yearly incidence is attributable to the variations in rainfall and evaporation that occur. Such areas are found mainly in the lowland parts of south-west Britain where temperatures are sufficiently high for development outside the final host to be easily completed in one season.

CLIMATE AND THE INCIDENCE OF FLUKE

In this way the geographical distribution of fascioliasis may be explained. In those areas where fascioliasis occurs climatic differences from year to year will determine its incidence. It has been shown that in these areas variations in wetness occur chiefly in May, June, July and August and that some three months of continuous development are required before cysts will appear on the herbage. Obviously a number of permutations may give rise to outbreaks and Table 19.5 shows some results from Anglesey demonstrating that some of these permutations do occur.

TABLE 19.5. *Weather conditions in Anglesey, North Wales*

Year	May	June	July	Aug.	Sept	Oct.
1925	W	D	D	D	W	W
1929	W	D	D	W	W	W
1933	D	D	D	D	D	W
1936	D	W	W	D	W	W
1947	W	W	D	D	W	W
1949	D	D	D	D	W	W
1954	W	W	W	W	W	W
1956	D	D	W	W	W	W

W = Rainfall exceeds evaporation
D = Evaporation exceeds rainfall

Should May, June and July be wet, cysts could be expected on the herbage during August. If May is dry but August wet they would appear during September. If May and June are dry but July and

* 'Dry' indicating that evaporation exceeds rainfall.

August are wet and the usual weather follows in September and October, cysts will be deposited during October If August is wet after a dry summer, then if the autumn is mild there may be some cysts on the herbage by early winter, but much of the infection would overwinter in the snail and cysts would appear on the herbage in the following summer if May and June were wet

The greater the succession of 'wet' months the more severe the outbreaks, years such as 1920, 1954 and 1958 when every month from May to October was 'wet' were disastrous years Sometimes in addition to September and October, June, July and August of one year are 'wet', with wet weather in May and June of the following year, in which case outbreaks begin in the early winter in one year and in the late summer of the succeeding year The outbreak in these two years is however, directly referable to the infection of one group of snails in one year An example of this was noted in South Wales in 1954 and 1955 This relationship in time between the various stages of the life cycle, which results from the interaction between the parasite and temperature (assuming moisture conditions are favourable) is represented diagrammatically in Fig 19 5 in order to clarify the difference between the summer and winter infections 'Dry' and 'wet' spells do not of course correspond with calendar months, nor are temperatures completely predictable so that many variations are possible Furthermore simple calculations based solely on the difference between rainfall and evaporation may be incorrect since the distribution of the rain throughout the month is an important factor Nevertheless, it would seem that by such processes as this, correlation between the level of fluke populations and climate can be derived One approach has been described for Anglesey by Ollerenshaw and Rowlands (1959) and its further development is leading to a system of forecasting epidemics in England and Wales

A consideration in the light of the above discussion of the control measures as advocated at present shows that they are completely inadequate What may be right in one part of the country may be entirely wrong in another, what may be right in one season may be wrong in the next For instance the source of infection in one year may be parent snails with overwintering infections, whilst in another it may be daughter snails from which cercariae will appear in the same year

The first stage in the control of the disease is treatment of infected animals. The use of carbon tetrachloride for sheep and hexachlor-

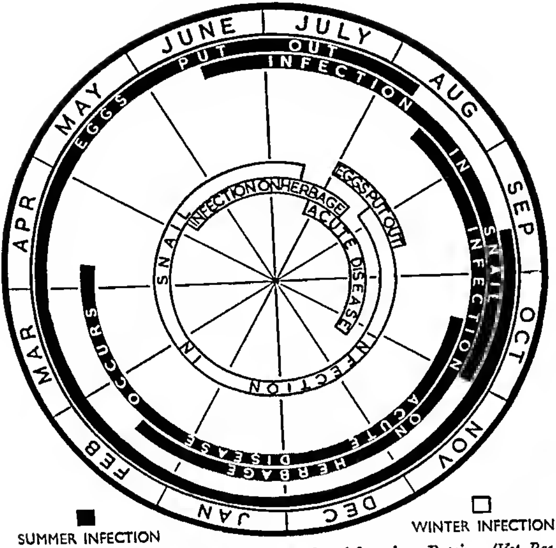

FIG. 19.5. Diagram showing the timing of the life cycle in Britain. (*Vet. Rec.*, 71, 962)

ethane for cattle is well known, but their use has its limitations in that immature flukes are not affected by the standard dose, whilst the dosing of sheep at lambing time and of milking cows is not advisable. Any prospect of eradicating the disease by increasing such treatment is therefore not considered practical particularly when the rabbit may be an important carrier of the adult fluke. The second stage in the control of the disease is preventing the animals from becoming infected. The effect of draining habitats has already been discussed and there is no doubt that expensive though this is, it is the only permanent answer. There are many areas where the topography and soil type render adequate drainage extremely difficult, particularly in very wet years; nevertheless it is interesting to record that great changes in fluke populations under these difficult conditions have been obtained by limited drainage operations.

The use of copper sulphate and more recently of sodium pentachlorophenate has been recommended for killing the snail and thereby preventing completion of the fluke life cycle. Little work on the effect of such treatment on natural populations of *L. truncatula* or of their recovery has been recorded. In Figs 19.6 and 19.7 some results of treatments are given. In our experience an application of 28 lb copper sulphate per acre gives about a 75 per cent kill, but it must be remembered that the application reduces the population pressure on the snails that are left so that, given suitable conditions, populations may be back to pretreatment level within twelve weeks. Indeed, under very favourable conditions, considerable increases above the original level of population have been observed. The use of molluscicides coupled with increase of environmental resistance by draining gives better results (Fig. 19.8), but in such cases the long-term effect is no better than that of drainage alone as a small residue of snails still remains. Since outbreaks may occur in the presence of only small densities of snails, the use of molluscicides on this basis seems to offer little prospect of success in preventing the disease. The emphasis in the use of molluscicides has hitherto been on killing snails when they were either most numerous or about to breed. Because of the long time required

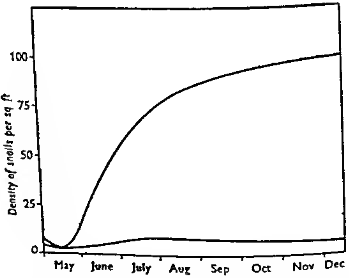

FIG. 19.6. The effect of an application of copper sulphate in May on two populations of *L. truncatula*. The habitats were sampled in May (before and after treatment) and again in August and December

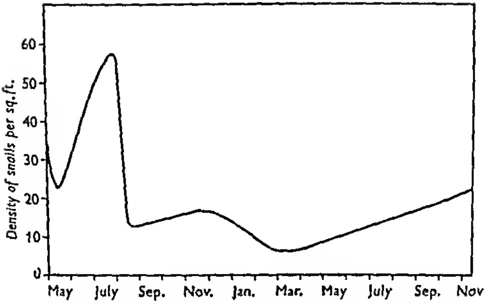

FIG. 19.7. The effect of applications of copper sulphate in May and August on a population of *L. truncatula*. The habitat was sampled in May and August (before and after treatment) and again in December, March, May and November.

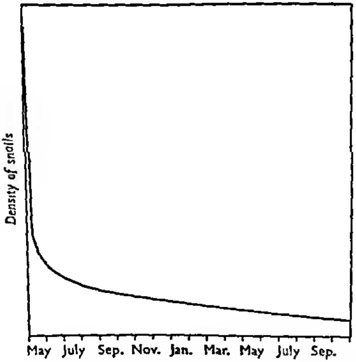

FIG. 19 8. The combined effect of copper sulphate and drainage on a population of *L. truncatula*. The habitat was sampled in May (before and after treatment) and again in September, March and October.

for the completion of the life cycle of the fluke it is usual for this to happen only once in each year, so that there is usually only one group of snails which produces the infection in any year The application of molluscicide should therefore be directed against infected snails before they have produced their infection on the herbage, and it is considered that to kill 75 per cent of the infected snails before they have produced their infection would substantially reduce the severity of an acute outbreak with the result that it could be controlled by dosing with carbon tetrachloride

An appreciation of the epidemiology as discussed here gives some indication when the molluscicide should be applied in March or April if it is to kill an overwintering infection, in August if early summer is wet, in September if late summer is wet, or not at all if it is dry throughout the summer Similarly, the timing and frequency of dosing stock should depend on climatic conditions during the summer Also the movement of stock to fluke-free fields and the fencing-off of habitats could be undertaken with regard to the expected time of deposition of fluke cysts on to the herbage Experience on one farm in Anglesey during 1958, a particularly bad year for acute disease, has shown that this approach can substantially reduce losses

Control measures of this kind obviously require considerable knowledge of the epidemiology of fascioliasis on the part of the flockmaster and his advisers, and this in itself constitutes a great difficulty in control At the same time it would be very wrong to suggest that the epidemiology of the disease is as yet thoroughly understood or that simple generalized recommendations can be formulated which would be effective in controlling the disease

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CHAPTER TWENTY

The Helminths of the Horse in Relation to the Pasture

D POYNTER

Introduction—Helminthiasis—Parasite control on pasture, in the horse—Dung disposal—Control of pin-worms and tapeworms—Conclusions

There are more than fifty species of roundworms that are capable of living within the horse They lay eggs which are passed, with the dung, out on to the pasture and when it is realized that the dung may contain upwards of 1,000 eggs in each gram it is not surprising to learn that estimates have been given that 40 horses might pass out 538 million eggs per day The amount of pasture infestation may indeed be prodigious and it is the aim of this chapter to consider those methods which may be adopted to control the level of the parasite on the paddock

For practical purposes it is proposed to divide the roundworms of the horse into three groups The first includes one species, *Parascaris equorum*, the large white roundworm that lives in the small intestine. This parasite produces eggs which are passed in the dung on to the pasture where they embryonate and become infective but do not hatch Horses become infected by ingesting the eggs The second group comprises a multiplicity of species which are for convenience called the small strongyles The common members of this group are *Trichonema* spp, *Triodontophorus* spp, *Poteriostomum* spp, *Trichostrongylus axei* and *Gyalocephalus capitatus* The members of the third group, the large strongyles, are *Strongylus vulgaris* and *S edentatus* as well as the now rather rare species *S equinus* All the strongyle worms produce eggs which hatch on the pasture to produce motile infective larvae

There are other species of worms living in the horse that do not conveniently fit into the above groups. The pin-worm, *Oxyuris equi*, lives in the colon and rectum where the females pass eggs out with the dung. The eggs embryonate but do not hatch until ingested by horses when they set up new infections. The female worms irritate the perineum and attempts on the part of the horse to rub the affected area on any convenient object may lead to dermatitis. Horses may also harbour tapeworms of the genus *Anoplocephala*. These worms live in the region of the ileo-caecal junction where they may produce ulceration of the mucosa. The eggs are passed in the faeces and ingested by pasture mites in which they develop. Infection of the horse occurs when it eats these mites.

The pasture as well as providing the natural food of the horse also provides a reservoir of infective material. With the intensity of equine breeding present in our studs today it follows that unless careful control is exercised the pastures cannot fail to become contaminated so that the parasitic diseases of the horse provide a real problem.

HELMINTHIASIS

Before mentioning the methods available to control parasitic diseases in horses it is necessary to discuss briefly the diseases themselves. Of all the worms that are mentioned above there is one, *S. vulgaris*, that is of greater pathogenic significance than all the others. *S. vulgaris* migrates in the arteries of the horse where it produces arteritis, especially in the region of the cranial mesenteric artery. The parasite is also responsible for coronary thrombosis and colic. Every year foals die as a result of *S. vulgaris* in their arteries. The disease is initiated by migrating larvae against which there is as yet no recognized treatmenr. So until such treatment is available or until such time as it is possible to immunize foals it follows that the only method on hand to combat the disease is one of control.

S. edentatus also undergoes an extensive migration involving the parietal peritoneum whilst small strongyles have relatively limited migrations, being restricted to the gut lumen or layers of the gut. Apart from the damage done by the migrating worms it is undesirable to have horses harbouring large burdens of adult worms in their intestines.

Parascaris equorum migrates by way of the liver, lung, trachea and oesophagus to the small intestine. Foals are often found harbouring

400 or so of these large worms and cases are on record of ascarid burdens causing perforation of the small intestine

Although we have a good idea of the pathological lesions produced by *S vulgaris*, little attempt has been made to study the effects of the individual strongyle species, but accounts have been published of the gross effects of a mixed strongyle infection (Archer and Poynter, 1957) Such infections produce anaemia and retardation in weight gain Although much is lacking in our knowledge of helminthiasis as it affects the horse, enough is known to show that the problem is a serious one and if the only parasite of the horse were *S vulgaris* the control measures about to be described would still be essential

PARASITE CONTROL

The problem of the parasite on the pasture is one which effects all horse owners but it is to the thoroughbred-breeders that the acute aspects of helminthiasis are more likely to present themselves in the way of valuable foals dying suddenly as a result of *S vulgaris* in their arteries The development of helminthiasis is, however, usually gradual, progressing as worms migrate in the body and intestinal burdens increase

The pastures of our stud farms are in the main used by mares, foals and yearlings Once a horse becomes a two-year-old it commences training and for the rest of its racing life it does not normally live at pasture Mares arrive at studs 'in foal', once there they 'foal down' and are subsequently served Mares often arrive bearing heavy worm burdens and eventually they are put out to pasture with their new foals Although those responsible fot the care of the mare may have sent her to the stud after anthelmintic treatment, such limited control is far from adequate One mare with a high burden or ten mares with low burdens can easily provide enough infective material to make foalhood hazardous even if the animals concerned are grazing on an erstwhile clean paddock

There are two places in which the parasite may be attacked First an attempt may be made to exercise control of the free-living stages on the pasture and secondly the worm burden within the horse may be controlled by anthelmintics

CONTROL OF THE PASTURE

Once a given pasture has been grazed by horses it will harbour the infective nematode stages put out by those horses In theory there

are four methods by which the nematode burden on a contaminated pasture may be reduced: (1) deep ploughing and reseeding; (2) rest; (3) treatment of the pasture by chemical substances; (4) mixed grazing. Consideration will also be given here to (5) harrowing, and (6) the manual picking up of faeces.

Ploughing and reseeding. This method is employed when it is known that a given pasture has been grazed by horses known to be passing out with their dung quantities of infective material. It may be assumed that any group of horses will, providing they are not under careful and consistent anthelmintic control, put on to the pasture large quantities of infective stages. The recommended procedure is to plough for a depth of at least nine inches and then to reseed, the principle being that the parasitic eggs and larvae will be deeply buried and not be able to survive and work their way up to become available on the subsequent herbage. It is debatable whether even this drastic treatment is completely effective. Such a step obviously renders a paddock temporarily useless as a pasture and although worth while for parasitic control it is often found that when consideration is given to other important factots it is impractical.

Rest. Many of the recommendations made for the control of the parasite on equine pasture are made on the basis of similar work conducted on sheep or cattle pastures, and whilst they are probably valid it must be borne in mind that we are dealing with different nematodes and that in this case extrapolation may be misleading. An examination made on a Newmarket stud farm one year was particularly interesting. The paddocks in question had from the spring to the early autumn been grazed by adult horses under no anthelmintic control. It was obvious then that a large amount of infective nematode material had been put on to them. An answer was wanted to the question, 'Will these paddocks be fit for foals next season?' During late autumn the paddocks were examined on at least three consecutive mornings. Employing the technique described by Crofton (1954) it was impossible to find appreciable numbers of infective larvae. In fact, in the whole examination the only parasite found was one infective larva of the genus Trichonema. The technique was working as was shown by the recovery of free-living nematodes. At the time of the inspection we had just experienced a summer of prolonged sunshine and the soil on the paddock was described by the stud-groom as 'baked'. In this case the owners were advised that the paddock would be suitable for next year's foals, but they were cautioned that the mares should be

carefully controlled. It is therefore reasonable to conclude that if a given pasture is rested during a hot dry summer and for the next winter, it will not have on it large quantities of parasitic nematodes. As a general rule it is advisable for foals to use paddocks that have been rested for at least a season and not to let them graze pasture previously utilized by other horses.

Treatment of the pasture with chemical substances. There is as yet no known method of controlling the population of infective nematode stages on a pasture by chemical means. Much work has been carried out on this aspect, but no effective inexpensive chemical has yet been found. Until it is we must look to the other methods outlined in this chapter.

Mixed grazing. Cattle parasites do not infect horses and equine parasites do not infect cattle. This fact forms the basis of control by mixed grazing. A pasture which has been used for horses is subsequently used for cattle which ingest and destroy many of the equine infective larvae and ascarid eggs. By employing this method of alternate grazing between cattle and horses, pasture infestations are not allowed to reach high figures. There is one parasite *T. axei* which is unaffected by mixed grazing since it is able to live in both horses and cattle. Fortunately this worm is of little pathogenic significance in horses so that mixed grazing has no drawbacks and is a method to be advocated. It is used on several Newmarket studs and no case of parasitic gastritis due to *T. axei* has yet been diagnosed.

Harrowing. It is as well here to mention the practice of harrowing. It is often stated that harrowing is a worth-while part of worm control in that the dung is broken up and spread around the paddock and that the nematodes in the dung are thereby exposed to adverse climatic effects. Even if this is so it must be remembered that such a practice will spread infective material over the whole paddock. It is well known that horses graze in a selective manner. In a paddock occupied by horses for any length of time it is easy to see that they defaecate in certain areas and graze in others. This phenomenon is well seen at times when pasture growth is at a low level. During several summers pony mares were noticed scratching around almost barren pasture when only a few yards away were patches of luxuriant growth. On closer examination it was seen that quantities of dung were present in the long grass but that none were present where the ponies were eating. There is evidence, then, that horses will not graze near their dung but away from it. Harrowing could upset selective feeding. The

method is obviously inferior to the manual picking up and disposal of faeces.

The manual picking up and disposal of faeces. There is one simple step that is of paramount importance in any method of pasture control and this is the manual collection of faeces. The dung should be removed from the pasture once or preferably twice a week. This method is rigidly employed on some well-managed studs and it is known to be effective. The strongyle eggs in the dung take, under normal conditions, about ten days to hatch and progress to third-stage infective larvae, so that if the dung is picked up before this period has elapsed pasture contamination is prevented.

Consideration has been given above to those steps which may be applied at least to reduce pasture contamination. Ploughing and reseeding is to be recommended, but it is too drastic to be employed as a routine procedure. Resting a pasture from late summer to the next spring is a convenient practical step and allowing cattle to graze after horses so that they act as larval clearers is another method of choice, together with the manual collection of faeces.

CONTROL OF THE PARASITE IN THE HORSE

So far consideration has been given to those methods which do not involve the actual administration of anthelmintics to horses, but it must be emphasized that it is within the horse that the parasites are concentrated. Any pasture attack involves combating a dispersed population but by treating the actual horses it is possible to kill a concentration of mature worms and prevent their subsequent reproduction. The chief source of infection to the foal is without doubt the mare. Mares and foals run together at pasture and even if the pasture is new it will, unless the parasitic population of the mare is controlled, support within a few days a larval level dangerous to foals.

The nematode population of the mare. Mares harbour in their intestines a diversity of nematode species with a tremendous reproductive potential. Some idea of the reproductive capacity of the worms is given in Fig. 20.1 which illustrates the egg counts of a group of pony mares kept at pasture (Poynter, 1954). It will be noticed that egg production increases rapidly during the spring and reaches a peak in the late summer after which a drop occurs so that egg production is again low during the winter. A similar picture to this is seen on thoroughbred studs. It is obvious that the number of eggs passed in the faeces of the mare increases at the time it is running at grass with its

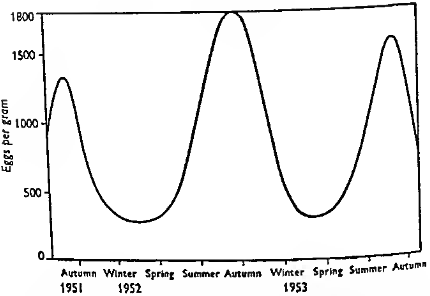

FIG. 20 1. The parasitic egg production of a group of pony mares kept at pasture. The seasonal fluctuation in the number of eggs passed is shown. Pasture infestations increase at the time when young foals graze with their dams, hence the necessity for the regular collection of droppings.

foal. Pasture infestations therefore increase at the time when the young susceptible foals are most in need of protection. It is such a state of affairs that leads to acute parasitism in the foal.

It is possible for mares to have egg counts in the order of 2–3,000 eggs per gm. of faeces and yet show no signs of parasitic disease. Providing the mare is on a good plane of nutrition there is little doubt that a large intestinal burden of adult worms can be tolerated. Any treatment the mares receive will be as much prophylactic treatment for the eventual benefit of the foal as it will be therapeutic treatment for the mare. It is important at this stage to realize that there is nothing static about a worm population. It is not merely a matter of removing the gut population and assuming all is well. Anthelmintics have no effect on worms undergoing their migrations. Gibson (1953) concluded that the development of large numbers of larvae is inhibited in the histotrophic stage and that they leave the mucous membrane of the caecal wall after the adult worms in the gut have been removed by an anthelmintic. There is in the adult horse a store of larvae living in the tissues waiting to enter the actual lumen of the gut. Thus one dose of an anthelmintic will only result in the replacement of an existing gut population by another one. Providing mares are not subject to

reinfestation it follows that repeated anthelmintic treatment will gradually deplete the total number of worms in the body and such was Gibson's experience in the aged horses he used for his work. However, as conditions exist today it is likely that reinfection will occur and consequently further controls must be applied.

It is necessary at this point to discuss in some detail the best practical methods which may be applied to ensure that the mare is not a menace to the foal, keeping in mind the fact that it is easier to kill the worms in the horse than it is to kill them on the pasture.

About one month prior to the expected date of foaling every mare should receive a full therapeutic dose of phenothiazine and piperazine. It has been shown by Poynter and Hughes (1958) that such a mixture gives a much better kill of the large strongyles than that achieved by either anthelmintic alone. Piperazine is given at the rate of 10 gm. per 100 lb. body weight with a maximum dose of 80 gm., whilst phenothiazine is used at the rate of 3 gm. per 100 lb. body weight. This combination of anthelmintics will rid a horse of the vast majority of its gut-lumen strongyles and ascarids but it will not affect the histotrophic stages of these worms. It is good practice to dose the mare again using the same anthelmintics at the same rate ten days or so after the birth of the foal, i.e. after the next service. The mare with her foal at foot will now soon be going out to pasture and it is at this point that control treatment becomes necessary. The two full doses of the anthelmintic mixture will have considerably reduced the helminth burden, but no chances must be taken of the mare passing fertile nematode eggs in her dung.

Gibson (1945, 1949), Dimock (1949), and Todd, Hansen, Kelley and Wyant (1949) have all studied the effects of small daily doses of phenothiazine on the strongyle worms of the horse. If horses are fed 2 gm. of phenothiazine per day then there is a significant reduction in the number of strongyle eggs passed and there is also a suppression in the fertility of such eggs. Gibson (1960) recently reported the results of an experiment in which he fed one mare one gm. of phenothiazine daily prior to and after she gave birth to a foal. The strongyle egg count of the mare never exceeded 2 e.p.g. and the mare and foal were on a paddock upon which horses had not grazed for several years. Despite this the foal became infected and at a post-mortem examination performed when it was just over one year old 638 *Trichonema* spp. and 9 *S. vulgaris* worms were found. There is no doubt that after acquiring its initial infection the foal itself was responsible for pasture

contamination and its own subsequent reinfection The experiment well illustrated the fact that foals too must be put on to low-level phenothiazine and this aspect will be considered later There have been many variations of the low-level phenothiazine regime that have been recommended On the assumption that there may be long-term toxic effects it has been suggested that adult horses should be dosed at the rate of 2 gm daily for the first 20 days of any month and that they should receive no treatment for the remaining 10 or 11 days However, Hansen Todd and Kelley (1949) were unable to observe any pathological lesions in the liver, heart, lungs, kidneys and spleen of four horses which had received either 0 5 1 0, 2 0 or 4 0 gm of phenothiazine every day for 14 months There were no changes in the erythrocyte counts It has been found that 10 grams of phenothiazine given once per week has a similar effect on the reduction in numbers and fertility of nematode eggs passed in equine dung but that when given at this rate fertile nematode eggs appear after about six months Enough has been demonstrated to allow the recommendation of 2-gm doses This regime which has been widely used in the United States and in Great Britain is satisfactory Ten grams or 15 grams once per week will also work at least for the period prior to weaning

Accounts are just beginning to appear of worms carrying on their reproduction in the continued presence of low-level phenothiazine. Drudge Wyant and Elam (1955) suggested in studying horses which had been treated for four years with small daily doses of phenothiazine that certain species of small strongyles were relatively refractory to the effects of treatment Gibson (1960) reported one mare in which despite daily treatment with 1 gm of phenothiazine nematode egg counts of 200–400 were obtained He regarded his observation as isolated as it fortunately is, but it seems likely that we are seeing the emergence of equine nematodes resistant to phenothiazine It is not the province of this chapter to discuss fully this interesting and controversial topic but it does illustrate the necessity for employing the services of a laboratory to help with any control programme The faeces of the horses should be periodically checked to make sure that the control measures are proving effective and any breakdowns dealt with by employing full doses of phenothiazine and piperazine together with making any pasture changes which become necessary Many questions asked by stud managers can only be answered by a knowledge of the nematode picture as reflected by faecal examination.

Whilst discussing the nematode population of the mare it is important to emphasize that any new arrivals on a stud should be isolated before being turned out to grass. Horses must only go to grass when they have received full doses of the anthelmintic mixture and when they are on the low-level phenothiazine regime. One horse with a high egg count grazing one pasture for one day can contaminate that pasture and make it unsafe for foals, thus undoing something which it may have taken months to attain.

The nematode population of the foal. The foal is born free of worms but from its first days on the pasture it begins to pick at herbage and thus it meets its first parasites. These undergo their greater or lesser migrations and arrive back in the gut again where they commence egg-laying and consequent pasture contamination. The first worm to reproduce and give rise to eggs in the foal's faeces is *Strongyloides westeri*. This parasite is common in foals and it produces quantities of eggs in the faeces. It has yet to be shown conclusively to be pathogenic and although some workers have suggested that it causes scouring it is relevant to note that out of 143 animals at Newmarket found to be harbouring the parasite only 13 (9·0 per cent) were scouring. The eggs of the parasite are found in the faeces at about 1–4 weeks of age and

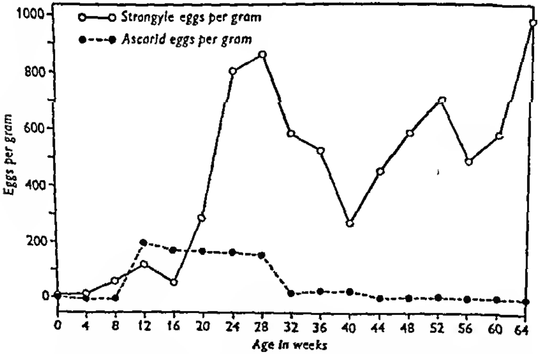

FIG. 20 2. The average nematode egg counts of a group of foals plotted against their age in weeks. The animals were kept at grass and no anthelmintic treatment was given.

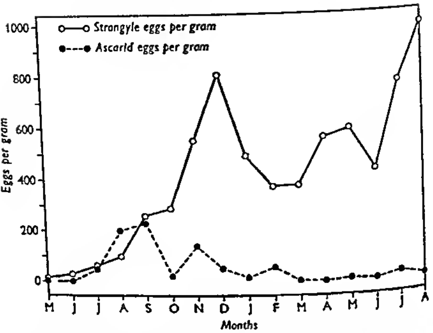

FIG 20 3 The same data as that given in Fig 20.2 plotted to show the seasonal fluctuation in the egg counts of the faeces of young horses

reach high figures, up to 24 000 e p g , during the first three months of life after which a sharp drop occurs so that the incidence in yearlings is a mere 0–4 per cent The parasite is a skin penetrator but since it presents no great problem it is beyond the scope of our present consideration.

At about eight weeks of age the first eggs denoting true infection with small strongyles appear in the faeces of the foal Strongyle eggs may be seen before this time, but they are probably due to the coprophagic habits of the young foal. Figs 20 2 and 20 3 illustrate the build-up of strongyles and ascarid infections in the foal The results were all obtained by studying pony foals at grass and no anthelmintic drugs were at any time administered It will be seen that the strongyle egg count rises during the first few months of life and reaches a peak at about 28–32 weeks, after which it falls only to rise again during the following spring Ascarid eggs were first seen at about 9 weeks of age and persisted for about six months after which their numbers declined. Should the egg production of the parasite within the foal remain unchecked, then it is apparent that a very considerable degree of pasture contamination will result.

The first eggs of the large white roundworm (*Parascaris equorum*) are

seen in the foal's faeces at 9–11 weeks of age. The foals are infected by ingesting eggs. The incidence of the parasite in adult horses is very low and even if mares are given full doses of piperazine, which is known to be 100 per cent efficient against this species, twice before foaling their foals still become infected. There is no doubt that the chief source of pasture contamination with regard to this species is the foal itself. Foals probably obtain their initial infection by ingesting eggs put on to the pasture by previous generations of foals or yearlings. The treating of foals for ascarids serves a dual purpose since as well as eliminating the ascarid population of the small intestine it also prevents pasture contamination.

When the foal is about 9–11 weeks old, the eggs of the small strongyles are first seen. Ascarids and small strongyles are both susceptible to piperazine and so there is no point in treating young foals with a mixture of phenothiazine and piperazine. Piperazine is given at the rate of 10 gm. per 100 lb. body weight and the first treatment should be given at about eight weeks of life so as to affect the ascarid and small strongyle burdens before they become established. Subsequent treatment will be necessary of course to eliminate any further worms which arrive; faecal examinations will reveal the need for this. If it is not possible to arrange such checks then it is as well to re-treat at an interval of four weeks, i.e. at about 12 weeks of age. Between the 20th and 25th week of the foal's life, the first members of the large strongyles begin to arrive in the gut, and consequently, once a foal reaches this age it is necessary to employ a mixture of piperazine and phenothiazine since such a mixture gives better results than either anthelmintic used alone.

It is difficult to prescribe a routine of anthelmintic treatment to suit every foal, since they obviously pick up infections at different rates. As a general guide it is advisable to treat the animal with piperazine in the 8th, 12th, 16th and 20th week of life. Due to the presence of the large strongyles after the 25th week any subsequent treatment should be carried out with the mixture. The first treatment with this mixture is required on the 25th week of life. There is obviously no point in prescribing low-level daily phenothiazine treatment for foals below the age of 8 weeks since it is not until they reach this age that they have present within their intestine their first egg-laying strongyles. If the piperazine treatments mentioned above are given then, there is no need for low-level phenothiazine for the week following each treatment with piperazine. As has already been mentioned, Gibson (1960)

recently demonstrated that even if a mare was kept on low-level phenothiazine at the rate of one gm per day a strongyle infection could still develop in her foal He showed that the number of eggs passed in the mare's faeces was very low, never rising above two per gm., but that the foal picked up a small infection presumably from these eggs This infection matured so that the foal became infected with larvae from the eggs it had itself produced The mare and foal grazed a paddock that had not been used by horses for a number of years and the mare was put on to the paddock prior to foaling and after her egg count had been reduced to zero It is true that the foal only contracted a small infection, but the results show the potential danger of leaving foals untreated It is a wise precaution to supplement the full doses of piperazine which are recommended at monthly intervals with courses of low-level phenothiazine at the rate of 1 gm. per day After a dose of piperazine and phenothiazine there is no need to treat for one week after which low-level daily phenothiazine should be started and this course will finish when the next full dose is given.

DISPOSAL OF DUNG

The proper disposal of manure from stables and yards is obviously an essential part of sound management Fresh horse manure must never be spread on horse pastures since it will disseminate infective eggs and larvae. The manure must be stored so that it ferments, the heat generated destroying the infective stages of the parasites If the manure is stored in open piles then the outer six inches of the exposed pile must be turned in every week so that it too is heated It has been shown that horse manure may be efficiently 'sterilized' by keeping it for two weeks in closed wooden boxes having double sides and double floors As a general rule, horse manure should be used on fields which are to be pastured by other animals or used for crop production

It must be remembered that after anthelmintic treatment many worms are likely to be passed in the faeces of the horses and that these worms will contain eggs If phenothiazine is being used then there seems little likelihood of such eggs producing infective larvae, but the same need not be true when considering worms passed after piperazine treatment. The two anthelmintics act in a different manner Worms passed after phenothiazine are usually dead, but those passed after piperazine are narcotized and if collected from the dung quickly they may be revived and produce fertile eggs It is therefore possible that a small portion of pasture could become heavily contaminated This

TABLE 20.1. *A summary of control measures which are applicable to stud farms and other premises where horses are kept*

(Further details of the individual items may be found in the text)

The Stud

Isolate new arrivals and treat with piperazine and phenothiazine	Foals on 'clean' paddocks	Every horse must be included in the programme. Barren mares and others not included below should be treated as yearlings

Mare

PTZ/Pip. — One month before foaling

Foals down

PTZ/Pip. — After next service

Low-level PTZ

Faeces examinations and further PTZ/Pip. treatment as indicated. If no examination possible PTZ/Pip. at least every two months.

Foal

Low-level PTZ

	Pip.	Pip.	Pip.	Pip.	PTZ/Pip.
Age (weeks)	8	12	16	20	25

Faeces examinations and further PTZ/Pip. treatment as indicated. If no examinations possible PTZ/Pip. at least every two months.

Yearlings

Low-level PTZ

Faeces examinations and further PTZ/Pip. treatment as indicated. If no examinations possible PTZ/Pip. at least every two months.

Once or twice a week pick up all dung	Intelligent disposal of dung	Mixed grazing	Rest of pasture—ploughing and reseeding

particularly applies to ascarids where the body may decompose leaving behind a quantity of fertile eggs How far this theoretical danger is real is unknown, but it does illustrate the importance of the intelligent disposal of dung passed after treatment

CONTROL AS IT AFFECTS PIN-WORMS AND TAPEWORMS

The control measures described above will have some effect on *Oxyuris equi* since it has a direct life cycle and further the adults are 75–85 per cent susceptible to mixtures of phenothiazine and piperazine. The tapeworms of the horse are not generally considered as dangerous, and there is a paucity of information with respect to the effect of anthelmintics They are not controlled by phenothiazine or piperazine, but will of course be subject to the other control procedures mentioned previously However, little is known of their ecology in relation to the pasture mite In any event they do not pose a serious problem

CONCLUSIONS

Table 20 1 illustrates the main features of a parasite control scheme but it must be emphasized that any effort expended must be unrelaxing or else control will break down. There are two places where the worm population may be attacked in the horse and on the pasture It is easier and more effective to attack worms in the horse and the current anthelmintics are capable, when properly administered, of ensuring that any dung passed will contain a minimum number of eggs However, anthelmintic attack must be coupled with sound pasture management so that the chances of dangerous infections building up are reduced to a minimum.

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CHAPTER TWENTY-ONE

Ectoparasites and Pasture

D W JOLLY

Introduction—Ticks the sheep tick, other ticks—The harvest mite—Attacking flies sheep maggot flies, warble flies, horse-bot flies, sheep nostril fly—Conclusions

Pasture, be it heather, heath or park land is a nursery and hunting ground for a vast population of insects, ticks, mites and other members of the phylum Arthropoda Salt and his co-workers (1948) have estimated that at the end of the summer there may be some 14 000 million arthropods per acre of pasture The majority of these creatures are overlooked by the farmer because they cause him no harm those which do concern the farmer attack his livestock to take their blood, or feed upon their tissues Mammalian blood is probably unsurpassed as a complete and concentrated food, and provides the sole nourishment for a wide variety of arthropod species varying from the larval tick to the horse fly (*Tabanus* spp) Since the average mammal resents the attack which is the essential prelude to a blood meal, most blood-sucking arthropods obtain their food without causing the host animal immediate discomfort, or select those portions of the animal body from which they are not easily dislodged The horse fly, a robust blood-sucker with a painful bite, will take blood from the neck or withers, out of reach of the horse's tail or teeth Other species such as the sucking louse, become permanent residents on the body of the host and draw their blood painlessly There are occasions, however, when the lice become too numerous, with the result that the skin reacts to their presence and eczema develops The main tissue feeders as opposed to blood-suckers, are represented by the larval stages or maggot forms of the sheep blowfly, *Lucilia sericata*, of the warble fly, *Hypoderma*

species, and of the sheep nostril fly, *Oestrus ovis*. However, the most dangerous blood-sucking arthropods are the ticks which, as they possess eight legs, belong with spiders and mites to the class Arachnida. Ticks are a danger to livestock throughout the world because of the diseases they transmit. They are also intimately associated with the pasture upon which most of them spend the greater part of their existence.

THE SHEEP TICK

MacLeod (1939) lists thirteen species of tick which occur in Britain, none of which, however, is a serious pest, with the notable exception of *Ixodes ricinus*, the sheep tick (Fig. 21.1). In 1932, MacLeod and Gordon showed that the sheep tick transmitted the virus of louping-ill, an encephalomyelitis of sheep and cattle. The same tick has also been incriminated as conveying the causal agents of tick-borne fever and tick pyaemia of sheep, and redwater of cattle. For these reasons the habits of this tick have been studied by a number of research workers.

The sheep tick occurs mainly on upland moors and heath pasture where the ground cover consists of bracken, heather, rush and rough grasses of the *Nardus*, *Molinia*, and *Agrostis* species. However, there is little doubt that the main pasture requirement of the tick is a high humidity, and provided this is present, the nature of the soil vegetation is of secondary importance. Milne (1944) has shown that ticks will survive where the surface geology results in poor drainage. Arthur (1948), who has studied the sheep tick in Wales, also noted that a high moisture content was the essential factor in the free-living existence of the tick and that the flora of the soil was less important. He suggested that the sheep tick showed a preference for peaty soil, and described some salt marshes which were free of tick despite the fact that the adjoining land was infested. Milne (1944), however, found no consistent correlation between the distribution of the sheep tick and the soil pH, available phosphates, soil texture, or soil depth. It would appear, therefore, that the sheep tick only requires the protection of a moist 'mat' of vegetation in which to develop undisturbed from one stage to another and from whence to emerge to take its blood meal.

Ticks feed only at certain specific times of the year. Usually they appear on the bodies of grazing animals in April and continue to be

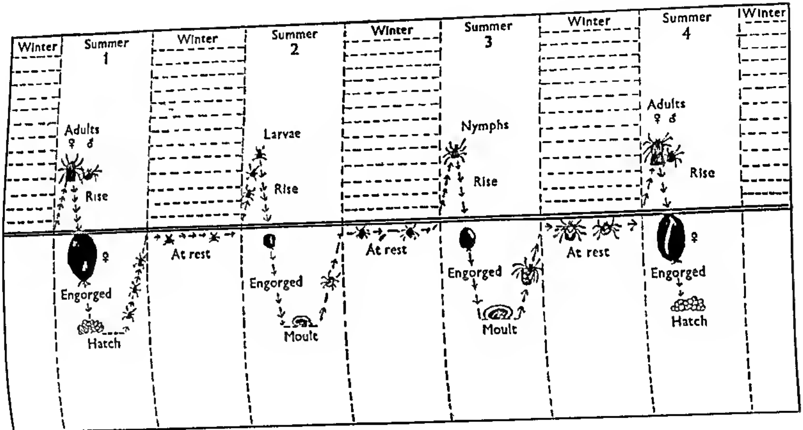

FIG. 21.1. Life cycle of the tick *Ixodes ricinus*.

present until May or early June. During the summer the animals are relatively free of ticks, until late August and September when there is a second, usually smaller, tick 'rise'. Sheep ticks do not feed during the winter. In some parts of Scotland, and also in mid-Wales, the ticks appear only once a year during June and July. Campbell (1949), to whom we are indebted for the description of the life history of the tick, considers that the sheep ticks become adapted by temperature into a spring or an autumn population and the spring ticks do not become active in the autumn or *vice versa*. The same worker suggests that 'summer' tick activity reported from some areas is caused by late stocking of the hill pasture, and is therefore really a late, or out-of-phase spring 'rise'. It appears therefore that all ticks search for a host once each year for 6–8 weeks.

The eggs of the sheep tick are deposited on the ground by the female, and appear as a cluster of some 2,000 brown globules, each of which is covered with a transparent, smooth, soft 'shell'. The incubation period of the eggs depends upon the temperature and humidity and varies from 3 to 36 weeks. The eggs hatch and the larvae which emerge are minute, almost colourless creatures with six legs. These larvae require some time to become accustomed to their environment and by the time they are ready to feed, the onset of the cold weather discourages any movement until the following spring almost one year after their birth as eggs. When the air temperature approaches 50° F. the larvae climb out of the mat of vegetation and swarm to the top of the rush, grass, or heather under which they have resided. At this time the ticks adopt a questing attitude with their forelegs extended before them like antennae. Stimuli such as would be associated with a passing host, i.e. sudden changes of light intensity, vibrations, animal smell and a heat source of 98°–100° F. will attract and excite the ticks (Lees, 1948). The efficiency of the tick in fastening on to the passing host was shown by Lees and Milne (1951) who collected approximately 50 per cent of all stages of the available ticks in a marked area by brushing the vegetation with their hands. The same authors found that ticks did not remain continuously at the top of the vegetation, but after a wait for 2–3 days they moved down on to a lower part of the stem, to return some days later to their former position at the top. The reason for these periodic wanderings is probably to allow the tick to restore its water balance which may have been depleted by exposure at the top of the plant. Most changes of position took place at dusk or dawn. This pattern of activity was followed for some 8

weeks after which, if it failed to feed, the tick returned to the ground where, in most cases it died from exhaustion Although ticks can live without food for as much as 31 months provided they are kept quiet, any movement will deplete their limited reserves of energy, and hasten their death

If, and when, the larval tick is successful in finding a suitable host such as sheep, cattle, rodent, bird, or indeed any warm-blooded creature, it punctures the skin with its mouth parts, and using this structure as an anchor becomes firmly fastened to the wound It proceeds to draw blood from the same site for 4–6 days When the tick is fully engorged with blood and literally blown out like a tiny balloon, it removes its mouth parts from the host and allows itself to be shaken to the ground The engorged larva, which is now dark blue in colour, disappears into the soil covering and becomes immobile, while the skin hardens to form a protective covering in which it moults for 6–37 weeks to emerge as a nymph or pre-adult This stage is somewhat larger than the larval stage and possesses the conventional eight legs of the arachnid

The nymph, like the larva, commences its hunt for food approximately one year after leaving its last host The same questing attitude is adopted at the tops of the vegetation If the nymphal tick is fortunate in finding a host, then it feeds continuously for 4–8 days until engorged with blood, when it detaches itself from the host falls to the ground and becomes buried in the depths of the mat of vegetation where the next moult is passed This metamorphosis lasts 10–20 weeks after which an adult male or female tick emerges

The male tick is chocolate brown in colour and has eight legs His function is to seek a host and pair with the female ticks There is approximately one male for each two females (MacLeod 1932) There is some doubt whether the male tick feeds at all during his adult life

The female tick is larger than the male Her abdomen is red in colour when unfed and is little more than a deflated bladder into which she will later pack a vast quantity of blood Both sexes of the tick seek a host, and behave on the herbage in the same way as that described for the other stages This takes place one year after the last meal and three years after the birth of the tick If the female tick is successful in finding a host, she makes her way to favoured sites for feeding where the skin is only lightly covered and tender, and sucks blood continuously for 7–11 days After she has been mated fully engorged

with blood, and changed in colour from red to blue, the female tick releases the mouth parts from the host and is shaken to the ground. Then she takes shelter and rests for 3–8 weeks before commencing oviposition. Egg-laying continues for several weeks, at the end of which the female dies.

The economic importance of the tick is due largely to the diseases it transmits during its parasitic existence. As a prelude to taking the blood meal, the tick pours the contents of its salivary glands into the host, and by this means injects the causal agents of louping-ill, tick-borne fever, or redwater. The ticks have themselves acquired these organisms by taking blood from other infected animals. The causal agents of louping-ill and tick-borne fever are collected by the tick larvae or nymphs and subsequently transmitted to other hosts at the next one or two feeds. The blood parasites which cause redwater in cattle can pass from the female to her eggs, and subsequently to the larvae and later stages.

The various stages of the tick are collected by sheep, cattle or other warm-blooded hosts as they move across, or rest upon, the pasture at the time of a tick 'rise'. In sheep, the ticks are found attached to those parts of the body where there is no wool. The ears, neck and chin, have been shown by Heath (1951) to be the most favoured area for tick attachment, probably because the muzzle of a grazing sheep is wiped across more vegetation than any other portion of the animal. Ticks which are collected by the host's forelimbs make their way to the axillae, and those gathered by the hind limbs climb on to the inside of the thighs. Cattle do not appear to collect sheep ticks around their face and ears, but carry the infestation where the hair is sparse on the inside of the fore and hind legs and around the udder. Nobody, to the writer's knowledge, has yet offered an explanation for the comparative absence of ticks on the face and ears of the cow, in contrast to the sheep. There is also an individual variation among both sheep and cattle in the tick burdens which they carry. An individual animal will often have a lower tick infestation than the flock or herd average, and it is a matter for conjecture whether such animals are less energetic and thereby pick up fewer ticks, or they are intrinsically less attractive to ticks.

The spring tick 'rise' coincides with lambing on the hill pastures. Newly born lambs are therefore, like their mothers, parasitized by ticks. The bites often cause severe skin abscesses, and may also result in tick pyaemia. This disease is characterized by abscess formation in

the joints and muscles and affects lambs 2–7 weeks of age It frequently necessitates the destruction of the lamb

The ticks cause some irritation and loss of blood whilst feeding Heath (1949) estimated that the blood loss per sheep during a heavy spring 'rise' of tick was approximately 1,400 ml The degree of irritation, as measured by skin reaction, varies with the individual and with the number of adult female ticks present There are hill pastures where over 100 female ticks can be counted on most sheep during the tick 'rise'

There is no doubt, therefore, that sheep ticks are undesirable inhabitants of pasture However, their removal is difficult and the most effective method is by harrowing, ploughing and reseeding Such an operation is unfortunately quite impractical on most hill grazings due to the rugged nature of the country Alternative methods of control such as heather burning, draining and the application of insecticidal dusts, sprays, or fogs to the pasture have proved valueless The present method of control aims at the protection of livestock by the application of an acaricidal dipwash, or cream, to the coats of grazing animals This method of control has been disappointing on cattle as their coats do not hold acaricides well and because the beasts remove much of the material by licking Sheep, however, can be protected against tick infestation for several weeks by dipping in gamma BHC or DDT and, more recently, certain organo-phosphorus insecticides. Such treatment must be carried out at the commencement of the tick 'rise' to give the maximum benefit On tick-infested pastures in the north of England and Scotland, tick dipping takes place in early April despite the fact that the ewes are about to lamb Nevertheless the ewes withstand complete immersion in a very cold acaricidal wash without ill effect The young lambs are protected against ticks within a week or so of birth by the application of acaricidal creams, dusts or by being bathed in a tub or dust-bin filled with a tick dip

Although the sheep tick will attach and suck blood from any warm-blooded host, Milne (1947) has shown that on the average hill pasture 98 per cent of the female tick population feed on sheep The efficient protection of sheep by the routine application of acaricides should therefore help to reduce the tick population on the pasture Heath (1949) was able to confirm this and removed the tick population from 12 acres of pasture by the repeated dipping of sheep grazing the experimental area. It would appear therefore that routine dipping of sheep in an effective acaricide is the best method of control at present

available in areas where ploughing and reseeding of grazing is impossible.

OTHER BRITISH TICKS

Although the other species of ticks found in Britain do not cause losses among sheep or cattle they can become a nuisance. They all three seek separate hosts on which to feed and spend their non-parasitic life on the ground. For many years Kent farmers have recognized a 'grass' tick, *Haemaphysalis cinnabarina var. punctata*. This tick, which superficially resembles the sheep tick, mainly infests the permanent pastures of the Romney Marsh, and attacks sheep and cattle. The 'grass' tick within the United Kingdom was generally considered as a unique and relatively innocuous part of the Kentish fauna. Recently, however, Marmion and Stoker (1958) have shown that this tick can carry the infective agent of Q fever, a disease of man which is often manifested as a pneumonia. Although the association between the Kentish 'grass' tick and Q fever has not been explained satisfactorily, it is interesting to note that the sheep tick *Ixodes ricinus*, and another British tick *Dermacentor reticulatus*, were free of this infection; 14 per cent of all pneumonias in man on the Romney Marsh were attributed to Q fever. *Dermacentor reticulatus* is well known on the continent of Europe, where it transmits disease to dogs and horses. In Britain, according to MacLeod (1939), the tick occurs in Devon, Somerset and Wales, but is not associated with disease.

Dogs and cats may be attacked by *Ixodes hexagonus* or *Ixodes canisuga*, both of which, as their name implies, resemble the sheep tick, *Ixodes ricinus*, and live in the pasture. *I. hexagonus* occurs mainly on hedgehogs, rodents and birds, but this tick is also commonly found in small numbers attached to the ears, face and neck of the household dog or cat.

prefer well-drained soils and are prevalent on chalk downlands The eggs are laid on the ground and hatch some 14 days later into red hairy larval forms with six legs Richards found that the larval harvest mite first appeared in late June, became most numerous in September and disappeared with the autumn frosts These parasitic mites are very active in dry sunny weather, but if this weather is dry for 2–3 weeks they tend to take shelter under bushes where the humidity is higher This fact may explain the countryman's association between harvest mites and currant or gooseberry bushes, in addition to cornfields. Having found a warm-blooded vertebrate host, the mite selects its site for feeding In rodents there is a preference for the ears, anus or genitalia, in the dog Steward (1943) found that the skin between the pads was frequently attacked, as are the heels of the horse In man harvest mites will often congregate where pressure occurs from clothing such as around the inside of a belt Jones (1950) has shown that the harvest mite fixes itself by its mouth parts to the skin of the host and uses its potent saliva to drive a hole in the skin by liquefying the epidermal cells The mixture of dissolved cellular material and saliva which is formed is sucked back to provide food for the mite and is a source of considerable irritation to the host The mites take 1–3 days to engorge after which they fall to the ground Harvest mites are not easy to control except by the application of an acaricidal cream containing gamma BHC or benzyl benzoate when the parasites are feeding on the skin

FLIES ATTACKING LIVESTOCK

The pasture itself has not so much effect upon the life history of the parasitic flies as it has in the case of the tick Nevertheless the pupal stages of these flies take place in the soil and the adult flies parasitize grazing animals All flies belong to the class Insecta and exist in the four quite different stages illustrated in Fig 21 2 of which the only two feeding stages are the larval (or maggot) stage and the adult stage Among the flies which attack livestock there is one stage only of each species which damages the host animal In the case of the horse flies and stable flies the adult takes blood and the larvae are non-parasitic and feed upon aquatic creatures or on horse manure Conversely the warble and bot flies do not feed at all as adults, but rely upon their larvae to acquire food from the body of the host animal

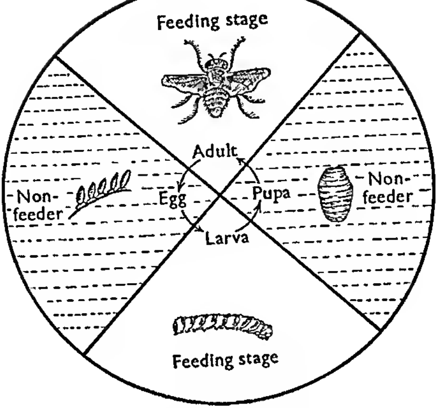

FIG. 21.2. Life history of a fly.

THE SHEEP MAGGOT FLIES

In the United Kingdom, the sheep maggot fly or green bottle *ucilia sericata* is the main cause of strike or myiasis in sheep. The :male fly is attracted to the sheep by faeces, urine or decomposing rganic matter held in the fleece and upon this the fly deposits her eggs. There are occasions however when these flies appear to need very little timulus to oviposit on sheep. The larvae or maggots, which emerge rom these eggs, make their way down to the skin, upon which they eed causing severe damage. The odour, mainly due to the excreta of he maggots, emanating from these lesions acts as a powerful attractant to other flies including the blue bottles or *Calliphora* spp. The affected sheep therefore becomes the target for a massive fly attack and will literally be eaten to death by maggots unless protected. The maggots feed on the sheep for 2–3 days then allow themselves to fall to the ground, into which they burrow, pupate and emerge as an adult fly some 14 days later.

The normal moisture content of the fleece is too low for the survival of eggs or the maggots; some factor which increases the humidity of the wool must therefore be present for a strike to develop. Apart

from contaminated wool, pasture with areas carrying lush grasses rushes, bracken or open areas sheltered by woods, and high hedges favour the survival of the flies, and the creation of a humid microclimate of the fleece (British Veterinary Association, 1955)

MacLeod (1956) has shown that *Lucilia sericata* is distributed throughout the United Kindom, and that the fly itself appears to be relatively unaffected by the vegetation cover The mature maggots are active soil borers and able to cope with most soil types and may travel for several feet through the soil before finally pupating In Britain the *Lucilia* spp may hibernate in this prepupal stage

One incidental factor which may affect the population of the maggot flies is the presence of predators, mainly beetles and ichneumid flies, which may destroy some 30 per cent of the pupae in the soil MacLeod quotes a report from Holland where it was noted that sheep on the newly reclaimed polders suffered from strike, although sheep on the neighbouring older polders were relatively free The suggested explanation for this phenomenon was that there was an absence of predators in the new polders

Sheep are protected from the unwelcome attention of the maggot flies by dipping or spraying with insecticides, of which dieldrin is the most effective and widely used in Britain

WARBLE FLIES

The ox warble fly relies upon its larvae to provide food for all stages There are two species, *Hypoderma bovis* and *Hypoderma lineatum*, the adults do not feed but devote their short lives of 3–4 days' duration to reproduction After mating, the female flies oviposit upon the hairs of the legs of cattle, and although the warble flies do not bite or sting their activity is resented by cattle The eggs of the fly hatch after some 3–6 days and the larvae crawl down the hairs, and burrow through the skin Having entered the body of its host in the late spring and summer, the warble larva commences a long migration towards the back One species spends December and January in the walls of the oesophagus but the other species over-winters in any one of a number of visceral organs However, both species of warble larvae reach the back of the host some time between mid-March and June, where they cause the formation of abscesses The larvae remain in the back for 10–11 weeks after which they emerge through a hole in the skin of the host originally made to allow the developing grub to breathe and fall to the ground. The warble fly larva then burrows into the soil and

pupates for some 30–40 days. This remarkable life history is still doubted by some farmers. However, recently both Canadian and British research workers have successfully reared generations of the two species of warble fly under carefully controlled conditions as part of an investigation aimed at controlling this troublesome pest, thus providing ample confirmation.

The application of derris washes repeatedly to the back at the time the warbles are present is the recognized and legal form of control in Great Britain. Certain members of the organo-phosphorus group of insecticides have also been shown to destroy the migrating larvae by a systemic action before they reach the back. Some of these compounds have been subjected to well-planned field trials in this and other countries indicating that a very high percentage of larvae are destroyed by one or two administrations during the winter. The eradication of warble flies may thus be considered as a future possibility.

THE HORSE BOT FLIES

Another group of flies which plague the grazing animal are members of the genus *Gastrophilus*. These insects, which resemble bees, attack the horse and lay their eggs upon the hairs of the host. Lapage (1956) records five British species of the fly, all of which have their own favoured site for oviposition, ranging from the cheek to the limbs. The larvae, which hatch from the eggs, ultimately attach themselves to the walls of the stomach. This location is reached by migration through the body of the horse as a result of being licked from the hairs, or by penetrating directly through the skin. The bot larvae remain in the stomach of the horse for 10–12 months. They are then passed through the alimentary tract and evacuated in the faeces on to the pasture. The pupal stage lasts 3–5 weeks and is spent within grassy tufts on the ground. The flies are active throughout the summer and are most prevalent on lowland pastures and parkland with tree cover, but it is the number of horses which influences their incidence rather than ground coverage.

The larvae can be removed from the stomach of the horse during the winter by the administration of carbon bisulphide. This is an irritant drug and is usually given in a capsule. More recently effective organo-phosphorus compounds have become available. However, most horses carry their winter burden of bots without any apparent ill-effects.

THE SHEEP NOSTRIL FLY

The sheep nostril fly, *Oestrus ovis*, does not lay eggs but deposits larvae around the nostrils of the sheep. The larvae move up into the nasal passages and sinuses and remain there for ten months When they have completed feeding the larvae are sneezed on to the ground, wherein they burrow and pupate, 3–8 weeks later the adult emerges It is doubtful if there is any association between types of pasture and the sheep nostril fly, for the presence of the host animal would obviously be the significant factor in their population density. A local heavy infestation of the fly is sometimes encountered, particularly in south-west England, without any obvious explanation.

In Britain control measures are seldom applied, but abroad, where the sheep nostril fly can be a serious problem, intranasal injections of solutions of acaricides such as gamma BHC or dieldrin are used

CONCLUSIONS

To the arthropod parasite the most important feature of any pasture is that it provides a host The disruption of the surface vegetation does not seriously disturb these parasites and even a population of sheep ticks is not much reduced unless there is a scarcity of host animals, such as would occur as a result of using the pasture for a corn or root crop Unfortunately the terrain carrying tick infestations is not usually conducive to the plough. The control of the warble, bot or maggot flies by pasture management is not practical owing to the short terrestrial existence of these parasites, as opposed to their long parasitic life These pests can only be controlled therefore by treatment of the hosts

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CHAPTER TWENTY-TWO

Enterotoxaemia

J J BULLEN

Morphology, cultural characteristics, antigens and toxins of Clostridium welchii *serological identification—Enterotoxaemia of sheep* (Cl welchii, *Type D*), *pathogenesis, diagnosis and prevention—Enterotoxaemias due to* Cl welchii, *Type A*, Cl welchii, *Type B and* Cl welchii, *Type C*

Enterotoxaemia means literally 'intoxication from the intestine' The term is usually applied to a number of diseases of sheep, goats, calves and pigs caused by anaerobic bacteria of the *Clostridium welchii* group All forms of enterotoxaemia have the following characteristics in common the bacteria are often normal inhabitants of the intestinal tract, disease is initiated by a variety of predisposing causes, some known, some unknown, which precipitate a rapid multiplication of *Cl welchii* in the intestine, and death is due to the absorption of soluble toxins produced by the rapidly growing organisms

CLOSTRIDIUM WELCHII

MORPHOLOGY

Clostridium welchii are Gram-positive non-motile spore-bearing anaerobes generally appearing as thick straight rods 4–8μ long and 0 8–1μ wide Occasionally almost coccoid forms are seen, especially in rapidly growing cultures and pleomorphic forms can occur, including long filaments, bent and twisted forms and large round or oval spheres. *Cl welchii* possess capsules, although the amount of capsular material varies considerably among different strains (Keppie and Robertson, 1944) The spores are oval and situated in the central or subterminal

position and soon become detached from the bacterial rod in which they were formed. They will resist 80° C. for more than 1 hour and 97–100° C. for 1–3 minutes (Robertson, 1929). The spores of Type F strains, which are unusually resistant, will survive 100° C. for 1–4 hours (Zeissler *et al.*, 1949).

CULTURAL CHARACTERISTICS

Under anaerobic conditions *Cl. welchii* will grow on most of the common laboratory media. A useful liquid medium consists of 10 per cent papain digest broth containing 20–40 per cent of meat particles, pH 7·8. Before inoculation the tubes or bottles must be boiled for 15–20 minutes to remove dissolved oxygen. The meat acts as a reducing agent. Growth is rapid. Large quantities of gas are produced during the logarithmic growth phase; the meat particles become pink in colour. Very vigorous growth can be obtained in media containing glucose, or serum, or both. These media can be made anaerobic by the addition of a strong reducing agent such as 0·02–0·1 per cent sodium thioglycolate. Numerous media of this type have been described, especially for toxin production (see Keppie and Robertson, 1944; Brooks, Sterne and Warrack, 1957).

Milk media rapidly become acid with the formation of a clot that is disrupted by the gas produced, the so called 'stormy fermentation'. Not all strains produce this reaction and Smith (1955) points out that the reaction is all too common among the saccharolytic clostridia to be of any use for the rapid identification of *Cl. welchii*.

For surface culture the most useful medium for routine use is probably 5–10 per cent horse, ox or sheep blood agar. After 18 hours of anaerobic incubation most strains of *Cl. welchii* have a characteristic appearance. The colonies are 1–2 mm. in diameter with smooth or crenellated outlines. After 2–3 days the colonies may reach 3–4 mm. in diameter. Some show a raised pointed centre, and radial markings are commonly seen. The haemolytic reactions on blood agar have been well described by Brooks, Sterne and Warrack (1957). On ox-blood agar the alpha toxin which has diffused into the medium surrounding the colony produces an extensive incomplete haemolysis, usually surrounded by an area of darkening. Alpha toxin has less effect on horse cells, and a weak alpha toxin may not be detectable. Theta toxin produces a clear haemolysis on both horse and ox blood, the area of complete haemolysis being usually surrounded by a zone of partial haemolysis due to alpha toxin. Delta toxin produces a clear

haemolysis on ox blood but does not affect horse blood They also described a form of haemolysis which they have shown is not due to alpha theta or delta haemolysis, this non-α, θ, δ haemolysis was produced by some strains of all types of *Cl welchii*, sometimes on ox blood, sometimes on horse blood, sometimes on both

VARIATIONS OF COLONY FORM, VIRULENCE AND TOXIN PRODUCTION

Rough colonies of *Cl welchii* have an irregular outline, flat surface and are usually more transparent than smooth forms Keppie and Robertson (1944) working with Type A strains, emphasize the importance of the selection of smooth, even-edged colonies for maximum production of alpha toxin and for virulence Smith (1955) states that animal to animal passage of stock cultures almost invariably results in a marked increase in virulence Some workers have described a sudden disappearance in a strain of the ability to produce a particular antigen Dalling and Ross (1938) describe a Type B strain which continually gave rise to epsilon-deficient variants McGaughey (1933) described the isolation of two variants from a strain of *Cl welchii*, Type A The original strain was smooth The colonies of one variant were rough with an irregular outline and a filamentous edge This culture produced very little toxin Colonies of the second variant had flat spreading edges and were more granular than normal This variant was never perfectly stable although under observation for over three years It produced far more toxin than the parent strain

ANTIGENIC STRUCTURE

Six main types of *Cl welchii* have been described Classification is based on the type and number of well-characterized soluble antigens produced by these organisms in culture Some of these antigens are toxic Many have been studied in great detail though none have yet been purified Numerous other antigens, as yet undescribed, probably exist. Brooks, Sterne and Warrack (1957) argue that all *Cl welchii* should be classified within the framework of the four 'major' lethal antigens, alpha, beta, epsilon and iota There seems much to be said for this argument which would restrict the total number of types at present known to A, B, C, D and E Variations within these types would be classified by a description of the numerous 'minor' antigens possessed by the individual strains

At present this view is not generally accepted, the strains derived

from cases of *enteritis necroticans* in man being given the status of Type F. If classification had been based on the possession of 'major' antigens these strains would have been called Type C which differed from the 'classical' type originally described by being large in form, possessing spores which show unusual resistance to heat and lacking the δ, θ and κ antigens (Brooks, Sterne and Warrack, 1957).

The antigen structure of the *Cl. welchii* types is shown in Table 22.1 (from Brooks, Sterne and Warrack, 1957). Classification of the *Cl. welchii* types based on the possession of 'major' lethal antigens only is shown in Table 22.2.

TABLE 22.2. *Classification of* Clostridium welchii, *showing division into five main types on the basis of the four major lethal antigens*

Type	Major lethal antigens: Alpha α	Beta β	Epsilon ϵ	Iota ι
A	+	−	−	−
B	+	+	+	−
C (including F)	+	+	−	−
D	+	−	+	−
E	+	−	−	+

THE MAJOR LETHAL ANTIGENS

Alpha toxin. This is a lecithinase produced during the logarithmic rowth phase of a culture. All strains of *Cl. welchii* produce alpha oxin but the highest yields are obtained from Type A strains. The oxin is lethal to mice on intravenous injection and produces necrotic eactions in the skin, if injected intradermally into rabbits and guinea-igs. Free calcium ions are essential for the lecithin splitting and hae-nolytic activity. This toxin has been extensively studied and the ollowing references are suggested for detailed information: Oakley ind Warrack (1941), Oakley (1943), Macfarlane (1948, 1950), Van Heyningen (1941).

Beta toxin. A necrotizing lethal toxin produced by Types B, C and F during the logarithmic growth phase of a culture.

Epsilon toxin. A necrotizing lethal toxin produced by Types B and D as a non-toxic prototoxin during the logarithmic growth phase of a culture. The prototoxin is converted, usually in about 4–5 days, to toxin by proteolytic enzymes produced by the organism. Rapid conversion

of prototoxin to toxin can be induced by digestion by proteolytic enzymes such as trypsin (Turner and Rodwell, 1943)

Iota toxin A necrotizing lethal toxin produced by Type E strains This also is produced as a prototoxin during the logarithmic growth phase of a culture, and slowly converted to active toxin by proteolytic enzymes This prototoxin can also be activated by trypsin (Ross, Warrer and Barnes, 1949)

For a description of the 'minor' antigens of *Cl welchii* and further references on the subject, the work of Oakley (1943) and Oakley and Warrack (1953) should be consulted

SEROLOGICAL IDENTIFICATION OF CULTURES

An unknown culture can be placed in one of the five main types (Table 22 2) by simple neutralization tests with culture filtrates and known antitoxins using mice as the test animal (Table 22 4) The culture can be grown in 10 per cent papain digest broth plus meat particles or 1 per cent glucose broth as recommended by Oakley and Warrack (1953) The media should be inoculated with an actively growing culture, incubated in a water bath at 37° C for five hours and clarified by centrifugation Preliminary tests for toxicity are made by injecting two mice intravenously with 0 3 ml of supernatant fluid and two mice with 0 3 ml supernatant fluid which has been treated with trypsin (1 per cent Trypsin Pulv B D H) at 37° C for 30 minutes after adjusting the pH to 7–7 5

If the mice injected with the untrypsinsized supernatant die and those with trypsinized material live the culture does not produce epsilon or iota toxin. Deaths rarely occur after 48 hours and the original supernatant kept at +4° C is usually suitable for neutralization tests If the original toxin is weak a fresh culture must be made Deaths in the groups receiving trypsinized material do not necessarily imply the presence of toxins other than alpha, as alpha toxin may sometimes survive the trypsin treatment (Oakley and Warrack, 1953)

If any mice die within 1 minute of injection, toxin may be present in high concentration and the test material should be diluted about ten times before neutralization tests are carried out Sometimes, however, these very rapid deaths are caused by unknown non-specific substances in the filtrate which are usually only lethal in high concentrations The presence of non-specific deaths is shown by the survival of mice injected with the original material diluted 1 10, if toxin is present the mice will probably die within an hour or less

TABLE 22.3. *Antitoxins/units/ml.*

Antiserum type	α	β	ε	ι
A	60–100	<0·5	<0·01	<0·1
C	10–20	1,000–3,000	<0·01	<0·1
D	10–20	<0·5	100–300	<0·1
E	10–20	<0·5	<0·01	100–300

TABLE 22.4. *Neutralization tests for major lethal antigens*

Type	Antitoxin	Toxin	Untrypsinized supernatant. Results in mice	Trypsinized supernatant. Results in mice
A	No serum	α	+	− [any deaths due to undestroyed α)
	Type A serum		−	−
	Type B, C, D and E sera		−	−
B	No serum	αβε	+	+
	Type A serum		+	+
	Type C serum		− (late deaths due to ε)	+
	Type D serum		+	−
	Type C and D mixture		−	−
C	No serum	αβ	+	−
	Type A serum		+	−
	Type C serum		−	−
	Type D serum		+	−
D	No serum	αε	+	+
	Type A serum		− (late deaths due to ε)	+
	Type D serum		−	−
	Type C serum		− (late deaths due to ε)	+
E	No serum	ι	+	+
	Type A serum		+	+
	Type E serum		−	−
	Type B, C and D sera		+	+

+ = Mice die   − = Mice live

The following sera are required for neutralization tests (Table 22 3), 0 1 ml of serum is added to 0 3 ml of supernatant fluid and left at room temperature for 30 minutes before injection The unit values suggested are quite arbitrary, it is important only to ensure that the sera contain adequate amounts of specific antibody to known antigens and that the Type A serum contains more alpha units per ml than the Types C, D and E sera

The neutralization tests described should provide a practical and convenient technique for diagnostic purposes It must be emphasized, however, that more reliable results can be obtained by the techniques described by Oakley and Warrack (1953) and Brooks, Sterne and Warrack (1957) This entails the use of intradermal tests in guinea-pigs and *in vitro* tests for the numerous minor antigens The review of Oakley (1943) should be consulted for a detailed discussion on the methods of testing for *Cl welchii* toxins

ENTEROTOXAEMIA OF SHEEP DUE TO TYPE D

Enterotoxaemia or pulpy kidney disease is caused by *Clostridium welchii*, Type D All ages of sheep can contract the disease but it is extremely rare in lambs under 7 days old The highest incidence probably occurs between the ages of 3 weeks and 18 months The disease occurs wherever sheep are reared but the incidence is extremely variable and it is difficult to assess the overall losses that occur Bennetts (1932) stated that annual losses in Western Australia varied between 1 and 29 per cent, losses of 5–15 per cent being quite common Dayus (1938) recorded an incidence of 2 per cent among 15,768 unvaccinated lambs in New Zealand Gill (1933) also in New Zealand, observed a high incidence (12 5 per cent) in one flock but says that the average incidence on farms when the disease habitually occurred was about 4 per cent and he also quotes data reported by Hopkirk who recorded average losses of 5 per cent among a total of 32,000 lambs on 38 farms In England Menzies (1938) found that an incidence of 1–2 per cent was common among ewes, in one outbreak the death rate among lambs was 14 5 per cent and on another farm where the disease had occurred over a period of three years the average loss was 5 per cent Baughton and Hardy (1941) report losses varying from 1 to 30 per cent among lambs in Texas Heath (1955) found that 152 of 530 deaths in sheep examined at Bangor, North Wales, were due to enterotoxaemia and Menzies (personal communication) states that in 1956,

508 cases of enterotoxaemia were found among 5,518 sheep, lambs and sheep viscera sent to Veterinary Investigation Centres in Great Britain. The figures for the Veterinary Investigation Centres do not, of course, give an indication of the total losses involved as one case sent for examination may represent several deaths in a flock, but they indicate that enterotoxaemia is still prevalent in this country.

Considering the evidence as a whole it seems that average losses of from 1 to 5 per cent may be expected but in severe outbreaks the death rate may rise from 10 to 30 per cent.

SOURCE OF INFECTION

Clostridium welchii Type D was first isolated from infected sheep by Bennetts in 1932. He also found the organism in the abomasal contents of two healthy sheep and in the soil areas where the disease had occurred but not in the soil when the disease was absent. Wilsdon (1931), Montgomerie and Rowlands (1934), examined a small number of strains of *Cl. welchii* from normal sheep all of which were of Type A or non-toxic. Gordon (1934), using mixed cultures, demonstrated *Cl. welchii* Type D in the intestinal contents of a few acute cases of grass sickness in horses. Borthwick (1937) found only Type D in the intestinal contents of each of three guinea-pigs. Type D was isolated from the intestinal contents of two dogs and Type A from four dogs. Type A only was obtained from two rabbits and six human subjects. Watts (1938) examined 36 strains from normal sheep, all of which were of Type A. Taylor and Gordon (1940) examined a large number of strains from soil and the intestinal contents of man and various animals; of 196 strains from 43 samples of soil, 7 were of Type D, the remainder Type A, and of 1,147 strains from intestinal contents, 1,134 were of Type A, 3 of Type B and 10 of Type D. Of the Type D strains, 1 was from a sheep, 2 from a bovine and 7 from a domesticated rabbit. Bullen (1952) examined the alimentary contents of 100 normal sheep sent to a slaughterhouse over a period of a year; 46 contained Type D *welchii* in one or other parts of the alimentary tract. Positive cultures were distributed as follows: 19 in the rumen, 15 in the abomasum, 14 in the duodenum, 17 in the jejunum, 30 in the ileum and 22 in the colon; many animals yielded positive cultures from more than one site. Smith (1957) states that 90 per cent of a non-immunized flock of sheep may possess epsilon antitoxin in their sera.

It thus seems likely that a high proportion of normal sheep may be carriers of *Cl. welchii* Type D, a potential source of danger if conditions

occur which are favourable for the rapid multiplication of these organisms in the intestine

SYMPTOMS OF ENTEROTOXAEMIA

Deaths from enterotoxaemia usually occur rapidly once the animal becomes ill, and for this reason the symptoms are seldom seen Bennetts (1932) mentions that the period between the onset of recognizable symptoms and death is very short He described two types of the disease, one characterized by convulsions, the other by coma and quiet death In the first type the animal was seized by convulsions, lying on its side it showed more or less violent galloping motions up to the time of death with twitching of the muscles, rolling of the eyes, grinding of the teeth excessive salivation and later pronounced retraction of the head and neck. Death usually occurred in 2–4 hours The initial stage of the less acute type was characterized by a staggering gait The animal then lay down, there was evidence of hyperaesthesia, with salivation and champing of the jaws, blindness and coma followed Death occurred quietly, usually in 3–4 hours The convulsive syndrome was relatively uncommon and more frequently seen in lambs than in adult sheep

Gill (1933) describes three types of symptoms in lambs, 'hyperacute', 'acute' and 'subacute' In the hyperacute form the animal suddenly developed convulsions and died in a few minutes or lingered for an hour or so during which it showed hyperaesthesia, frequent convulsions and signs of severe pain with straining and bleating The symptoms of the acute type were similar to the hyperacute but less violent There was often a fairly rigid extension of the limbs with the head pressed back until it almost touched the shoulders Gill states that some of the animals might live for several days but rarely recovered In the subacute or lethargic form the lamb was found to be dull and listless, often wandering by itself Blindness was common After a while more acute symptoms might develop He makes the interesting observation that if the lambs were purged and then starved for 48 hours, they often showed a marked improvement If they were then given a large feed of milk they often relapsed, but might make a complete recovery if fed small amounts at frequent intervals

Baughton and Hardy (1941) also describe convulsive and comatose forms of the disease They mention that both types show a well-marked glycosuria They did not notice any diarrhoea

The description of experimental enterotoxaemia given by Bullen and

Scarisbrick (1957) corresponds closely to the acute type of the disease, although the experimental animals showed more severe diarrhoea than is generally noticed in the natural disease.

> Symptoms of enterotoxaemia usually appeared between ½ and 1¼ hours before death. The earliest signs consisted of slight trembling along the back and some uneasiness. This was soon followed by a rapid oscillating movement of the eyes. If the animal was held at this stage there was often a violent convulsion; the limbs were held at full stretch, the head and neck thrown backwards between the shoulder blades and the whole body was rigid and hard to the touch. A convulsion of this kind lasted some 5–15 seconds and was followed by collapse. Some animals had several convulsions, a few none. Towards the end the respirations became deeper and the animal lapsed into a coma. The corneal reflex disappeared, and the muzzle became wet with saliva. Strenuous paddling movements of the legs usually appeared shortly before death.

It seems likely that the differences in the symptoms observed in the 'convulsive' and 'comatose' types of the disease are due to the relative amounts of toxin absorbed, the absorption of very large amounts causing the more acute form of the disease.

POST-MORTEM LESIONS OF ENTEROTOXAEMIA

The majority of animals are in good condition and there is usually evidence of recent diarrhoea. The type and extent of the lesions observed very largely depends on the time that has elapsed between death and examination.

In experimental animals immediately after death there is usually a large excess (50–60 ml.) of clear fluid in the pericardial sac. The heart shows subendocardial and epicardial haemorrhages. The small and large intestine may be slightly congested. The intestinal contents are usually full of gas and there is evidence of a recent mucoid diarrhoea. The urine contains large quantities of sugar (Bullen and Scarisbrick, 1957).

Natural cases of the disease usually cannot be examined until several hours after death. The small intestine often appears congested and contains only a small amount of thick material which has the consistency of mayonnaise. The lungs are congested and there is often a pericardial exudate. Epicardial and subendocardial haemorrhages are almost always seen. The urine contains large amounts of sugar. The kidneys are extremely soft, sometimes almost liquid in consistency. This pulpy kidney lesion is a post-mortem change, which cannot be found

immediately after death (Bullen and Scarisbrick, 1957). Bennetts (1932) also mentions that two lambs which died from experimental enterotoxaemia had typical 'pulpy' kidneys when autopsied 3–4 hours after death. Two normal lambs killed by stunning and left for three hours had normal kidneys.

BLOOD GLUCOSE LEVELS IN ENTEROTOXAEMIA

Gordon *et al.* (1940) showed that sheep injected with lethal doses of *Cl. welchii* Type D filtrates developed a marked rise in blood glucose shortly before death. Lethal doses of *Cl. welchii* Type A and C filtrates did not produce this effect. These authors also found that the urine of cases of natural enterotoxaemia contained a great deal of sugar unaccompanied by albumen. Blood samples from a few cases showed that the sugar content was abnormally high, in some cases over 350 mg. per 100 ml. Glycosuria has also been reported in natural cases of enterotoxaemia in the United States (Baughton and Hardy, 1941).

Bullen and Scarisbrick (1957) found that all ten cases of experimental enterotoxaemia, except one which was not examined, showed a striking hyperglycaemia which was closely associated with the appearance of typical symptoms of the disease. Blood glucose levels rose from 50 to 70 mg. per 100 ml. to 130–300 mg. per 100 ml.

THE PATHOGENESIS OF ENTEROTOXAEMIA

The effect of the introduction of cultures of Type D into the rumen. For many years it has been recognized that enterotoxaemia might be initiated by a sudden alteration in the food supply, usually from a moderate or poor diet to a rich and succulent one. Nevertheless it was soon realized that the disease could not be reproduced easily with oral doses of cultures of *Cl. welchii* Type D.

Bennetts (1932) found that oral doses of culture were without effect. He thought that a low pH in the abomasum might destroy large numbers of ingested organisms and that the rapid passage of ingesta through the small intestine would prevent any accumulation of bacteria or toxins. He attempted to neutralize the acid in the abomasum with large doses of sodium bicarbonate and to reduce peristalsis of the small intestine with large and frequent doses of opium and belladonna. In these circumstances he was able to reproduce the disease in 4 out of 6 sheep. Oxer (1932) and Gill (1933) failed to repeat these results.

Roberts (1938) reproduced the disease in young lambs by feeding cultures of *Cl. welchii* Type D combined with large quantities of milk

powder and casein. The organisms grew well in the abomasum, but unfortunately it is not known if the organisms that passed into the intestine continued to grow and produce toxin or whether a sufficient dose of toxin accumulated in the abomasum and was later absorbed lower down the intestine. Shaw, Muth and Seghetti (1939) failed to reproduce the disease in lambs with oral doses of culture and sodium bicarbonate or with culture and a large feed of milk. Harshfield, Cross and Hoerlein (1942) apparently reproduced the disease in 3 of 8 lambs given cultures of a strain of *Cl. welchii* combined with a large feed of grain or milk. The strain of *Cl. welchii* had been isolated from a case of enterotoxaemia.

The frequent failure to reproduce the disease with oral doses of culture led Bullen, Scarisbrick and Maddock (1953) to follow the fate of washed suspensions of *Cl. welchii* Type D introduced into the rumen. Sheep were equipped with permanent fistulae in the rumen, duodenum and ileum. A large dose of organisms was introduced into the rumen and viable counts of these organisms made at intervals thereafter. It was also necessary to have some method of estimating the rate of flow of the intestinal contents as this would greatly influence the viable count. A radioactive marker consisting of Iridium 192, incorporated into alumina particles, was introduced into the rumen with the culture. These particles were insoluble and had the same suspension properties as *Cl. welchii.* The behaviour of the bacteria could then be followed by comparing the ratio of bacteria to marker particles, assuming that both particles and bacteria were carried along the alimentary tract at the same rate.

The results of two experiments are shown in Table 22.5. In the two

TABLE 22 5. Cl. welchii *Type D in the alimentary canal of normal sheep.* (*Ratio of bacteria to radioactive marker* Cl. welchii *Type D/gm /Counts/min./gm.*)

Time (hours)	Rumen		Duodenum		Ileum	
	Expt. 7	Expt. 8	Expt. 7	Expt. 8	Expt. 7	Expt. 8
1	5,720	9,200	<20	<24	17,000	—
3	1,110	4,100	<100	380	258,000	640,000
6	800	1,020	<5	100	7,500	20,000
9	93	124	<4	<5	2,060	11,000
12	8·5	36	<3	<5	1,380	4,600
15	—	—	—	<5	779	61

Inoculum ratio . expt. 7, 9,520 : 1; expt. 8, 20,200 : 1

experiments in which the marker was used it was calculated that at least 90 per cent of the bacterial inoculum was destroyed in the rumen It can be seen that in experiment 7 after 1 hour the ratio of bacteria to marker in the rumen was 5,720 to 1 but only 8 5 to 1 after 12 hours Only very small numbers of viable organisms reached the duodenum where the maximum ratio of bacteria to marker was 100 to 1 in experiment 7 and 380 to 1 in experiment 8 In the ileum there was evidence of a short period of rapid multiplication. In experiment 7 the ratio of bacteria to marker rose to 258,000 to 1 and in experiment 8 it reached 640,000 to 1, these figures indicate enormous bacterial multiplication in the small intestine This rapid multiplication was not maintained for long and the ratio of bacteria to marker then fell rapidly

Considerable amounts of epsilon toxin were produced during the period of rapid multiplication The maximum concentrations varied in different experiments from 20 to 2,000 mouse intravenous MLD per gm of ileum contents The toxin had no effect on the sheep, except in one animal which had a violent though transient attack of diarrhoea shortly after the toxin level had reached 2,000 MLD per gm This animal possessed no circulating epsilon antitoxin

The results showed that the intestinal contents of normal sheep provided a suitable substrate both for the multiplication of *Cl welchii* Type D and for the production of epsilon toxin Nevertheless, the rate of multiplication of the bacteria appeared to be insufficient to maintain their numbers in the intestine Thus the rapid destruction of the organisms in the rumen and the rapid flow of the intestinal contents, which removed any accumulation of bacteria or toxin, were believed to account, in part at least, for the resistance of normal sheep to large oral doses of cultures of *Cl welchii* Type D

The effect of a continuous dose of culture introduced into the duodenum As the introduction of a single dose of culture into the rumen was followed by only a transient multiplication of organisms in the small intestine, it was decided to try the effect of a continuous dose introduced directly into the duodenum Cultures containing $500–800 \times 10^6$ organisms per ml were dripped into the duodenum of normal sheep at the rate of 100 ml per hour, usually for 5–9 hours On one occasion the culture drip was maintained for 22 hours at the rate of 300 ml. per hour

It was found that normal sheep were surprisingly resistant to this treatment. Many developed short attacks of diarrhoea, but in others there was very little effect Some animals stopped feeding during

the experiment but were eating and drinking normally within 24 hours. When the sheep were fed on normal diets such as hay or hay and small amounts of oats and bran the viable count of *Cl. welchii* Type D in the ileum rose to a maximum of 1–700 × 10^6 organisms per gm. (Table 22.6). The counts usually declined rapidly as soon as the culture drip was stopped. It therefore appeared that the organisms were unable to multiply sufficiently fast to maintain their numbers in the intestine. This result was probably due to a lack of adequate substrate for rapid multiplication and also to the rapid flow of the intestinal contents.

TABLE 22.6. *Growth of* Cl. welchii *Type D in the ileum contents of sheep following the introduction of culture into duodenum. (1) Sheep fed on a normal diet of hay or hay and small quantities of oats and bran. (2) Sheep overeating on wheat, lucerne or oats*

	Experiment no.	Diet	Maximum viable count (organisms per gm.)	Time of maximum count after start of culture drip (hr.)	Fate of sheep
1	X11	Normal	93 × 10^6	31	Survived
	X20	,,	116 × 10^6	4	,,
	X35	,,	680 × 10^6	6	,,
	X36	,,	300 × 10^6	9	,,
	X37	,,	490 × 10^6	5	,,
	X38	,,	1 × 10^6	6	,,
2	X83	Overeating on wheat	2,500 × 10^6	4	Died of enterotoxaemia
	X71	,,	4,100 × 10^6	5	,,
	X70	,,	4,800 × 10^6	7	,,
	X69	,,	1,400 × 10^6	9	,,
	X12	Lucerne	1,140 × 10^6	9½	,,
	X18	Oats	13,500 × 10^6	17	Survived (immune)

The effect of a change of diet and overeating. The rumen flora of a sheep on a diet of hay consists largely of cellulose-digesting organisms. If the diet is changed, to wheat for example, the rumen flora must adapt itself to the new substrate. The cellulolytic organisms are gradually replaced by other organisms better adapted to fermenting wheat starch. It takes some time for the new flora to become established in sufficient numbers to ferment all the material entering the rumen. If at the same time the animal overeats, the rumen becomes filled with a mass of undigested starch which escapes into the small

intestine This provides an ideal substrate for the growth of *Cl. welchii* Type D.

In a few hours after the start of the culture drip the viable count in the ileum rose to over 1,000 × 10^6 organisms per gm This very rapid growth was maintained in spite of the development of a profuse diarrhoea, showing that the organisms were growing more than fast

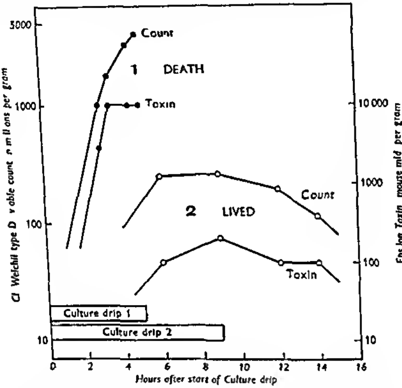

FIG 22 1 Experimental enterotoxaemia Growth of *Cl welchii* Type D and production of epsilon toxin in the ileum (Experiments X71 (1) and X36 (2), Table 22 6)

enough to replace the numbers washed out of the intestine (Table 22 6 and Fig 22 1)

The rapid growth of *Cl welchii* Type D was closely associated with the production of high concentrations of epsilon toxin This was not tolerated for long and the sheep soon died of acute enterotoxaemia There was a good correlation between the presence of undigested starch in the intestine and the successful reproduction of the disease All the successful experiments with sheep fed on wheat showed large numbers of starch granules in the ileum contents If the granules disappeared from the intestine, the continued introduction of culture

into the duodenum resulted only in a relatively poor growth of the organisms and failure to reproduce the disease. It was also found that if the diet was changed gradually from hay to wheat the rumen flora apparently had time to adapt itself successfully to the new substrate. No free starch then appeared in the intestine even if large amounts of wheat were eaten.

The absorption of epsilon toxin. Bullen, Scarisbrick and Maddock (1953) noticed that normal sheep could tolerate, at least for short periods, epsilon toxin concentrations in the ileum varying from 20–2,000 mouse intravenous MLD per gm. without ill effect. This suggested that epsilon toxin is not easily absorbed from the intestine. It was therefore felt important to investigate the circumstances which allow the absorption of this toxin to occur. The first experiments were done with mice. Bullen and Batty (1956) prepared two concentrated culture filtrates of *Cl. welchii* Type D which contained approximately 30,000 and 166,000 mouse intravenous LD 50 of epsilon toxin per ml.

It was found that normal mice were resistant to a large oral dose of toxin but if the dose were divided and given as a series of smaller doses the animal died with typical symptoms of epsilon toxin poisoning. The amount of toxin given was important. A lethal dose of epsilon toxin was absorbed in the intestine only if the toxin was maintained at a high concentration in the intestine for some hours. To ensure a 100 per cent kill in mice it was necessary to give five hourly doses of the first culture filtrate containing 16,500 intravenous LD 50 per dose, a total of 82,800 LD 50. The maximum toxin concentration in the intestine was approximately 5,000 mouse MLD per gm. Ninety per cent of this dose failed to kill all the mice and 10 per cent killed none. With the second filtrate it required 5 doses of 41,500 intravenous LD 50 per dose, a total of 207,500 LD 50 to kill all the mice.

Similar results were obtained with sheep (Bullen and Scarisbrick, 1959). More than a dozen normal sheep survived in experiments in which the toxin concentration rose to a few 100 MLD per gm. of ileum contents. In one case the culture was dripped into the duodenum for 22 hours. The toxin concentration in the intestine varied from 80 to 400 MLD per gm. for most of the time and rose to 8,000 MLD for a very short period. The sheep recovered completely, but a week later died with typical symptoms of enterotoxaemia when toxin concentrations varying from 4,000 to 20,000 MLD per gm. were maintained for approximately 5 hours. In every case in which

the disease was reproduced successfully high levels of toxin were maintained in the intestine for several hours on end (Bullen and Scarisbrick, 1957)

These results suggested that low concentrations of epsilon toxin, even for long periods, were harmless High concentrations of toxin were harmless if present only for very short periods Lethal amounts of toxin were rapidly absorbed if high concentrations were maintained for several hours on end

The effect of epsilon toxin on the permeability of the intestine The results of the early experiments with mice suggested that repeated doses of toxin might alter the permeability of the intestine (Bullen and Batty, 1956) This idea was investigated by using concentrated antitoxin as an indicator substance to detect any increase in permeability Adult mice given a large oral dose of antitoxin absorbed very small but constant amounts from the intestine Any increase in the rate of absorption would indicate an increased permeability of the intestine In all the experiments with mice five doses of a mixture of antitoxin and saline, or antitoxin and the concentrated filtrate were given at hourly intervals directly into the stomach The mice were bled at intervals The death rate was recorded after 24 hours

The experiments showed that lethal doses of concentrated culture filtrate caused a rapid increase in the permeability of the intestine An increase in permeability was detectable at the first bleeding, only 1½ hours after the first dose, between 4 and 23 times the amount of antitoxin found in the controls being absorbed into the circulation After 3½ hours the permeability of the intestine was increased still further

If the epsilon toxin in the filtrate was rendered inactive with specific antitoxin or destroyed by heating, the increase in permeability was invariably delayed and was not detectable after 1½ hours, but a considerable increase in permeability occurred after 3½ hours Neutralization tests with antitoxin provided good evidence that the early increase in permeability was due to epsilon toxin The delayed increase in permeability which was observed when the epsilon toxin was absent from the filtrate showed that some other factor or factors were present in the filtrate capable of causing an increase in permeability This factor was not present in uninoculated broth and must have developed during the growth of the culture

Similar experiments were done with sheep (Bullen and Batty, 1957) The rate of absorption of concentrated diphtheria antitoxin was used to assess the permeability of the intestine in normal sheep and those

dying of experimental enterotoxaemia. The antitoxin mixed with saline or cultures of *Cl. welchii* Type D was introduced directly into the duodenum. The animals were then bled at intervals from the jugular vein. In every case of fatal experimental enterotoxaemia in which this system was used the permeability of the intestine was increased. This was shown by the increased rate of absorption of diphtheria antitoxin compared with the controls which were dosed with antitoxin and saline only. The greatest increase in permeability occurred in two animals in which the antitoxin was added to the culture drip towards the middle or end of the experiment when high concentrations of epsilon toxin had been present in the intestine for some hours.

Overeating disease and enterotoxaemia. Smith (1957) states that enterotoxaemia is almost always associated with a heavy intake of nutritious food, such as milk, fresh grass or grain. Bullen and Scarisbrick (1957) found that overeating played an important part in the development of experimental enterotoxaemia, and that the introduction of cultures of *Cl. welchii* Type D into the intestine without overeating appeared to be harmless.

Nevertheless there appears to be some difference of opinion on the exact role played by overeating in actual outbreaks of enterotoxaemia. Britton and Cameron (1944), for example, considered it unlikely that the absorption of *Cl. welchii* epsilon toxin was responsible for the disease. This confusion appears to have arisen from the fact that it is quite possible to produce a severe and sometimes fatal acidosis in sheep by feeding large quantities of carbohydrate (C.S.I.R.O. Reports, Australia, 1948–9, 1950, 1951 and 1952; Hungate *et al.*, 1952). The severe acidosis which may occur some 12–24 hours after a large feed is due to the very rapid growth of acid-producing organisms in the rumen, usually *Streptococcus bovis.* Death can occur after 1 to 3 days.

Bullen and Scarisbrick (1957) distinguished experimental enterotoxaemia from death due to overeating and acidosis by the following criteria. Death from acidosis in animals fed with large quantities of wheat occurred after periods varying from 25 to 65 hours. Typical symptoms were dullness and inappetence followed by sudden collapse shortly before death or a prolonged weakness and prostration, with hyperventilation and salivation followed by coma and death. On the other hand most of the animals dying of enterotoxaemia showed typical nervous symptoms with convulsions. The interval between

the appearance of typical symptoms and death was short, not more than $1\frac{1}{4}$ hours Of the ten animals killed with experimental enterotoxaemia five showed no symptoms of acidosis The remaining five animals showed only mild symptoms of acidosis and three died within six hours of the start of the culture drip The clearest differentiation between the two conditions was shown by the behaviour of the blood glucose All the animals dying from enterotoxaemia, except one which was not examined, showed a marked hyperglycaemia which was closely related to the appearance of typical symptoms All the animals dying from acidosis showed normal blood-glucose levels immediately before death

Summary, Pathogenesis of Enterotoxaemia The organism responsible for enterotoxaemia of sheep, *Clostridium welchii* Type D, is a common inhabitant of the alimentary tract of normal animals

The disease cannot be reproduced in sheep fed on normal diets such as hay even if large quantities of *Cl welchii* Type D are introduced into the intestine for long periods of time This appears to be due to the following factors the absence of large quantities of fermentable substrate in normal intestinal contents limits the growth of the organisms, the rapid flow of the intestinal contents soon removes any accumulation of bacteria and toxin, the toxin is not easily absorbed and low concentrations are harmless

The disease can be reproduced consistently if the diet is changed suddenly and large quantities of rich food such as wheat are eaten before the culture is introduced into the intestine In these circumstances the rumen flora cannot adapt itself sufficiently rapidly to the changed environment and large quantities of undigested or partly digested food escape into the small intestine. This provides an ideal substrate for *Cl welchii* Type D which grow extremely rapidly and produce high concentrations of epsilon toxin High concentrations of toxin and possibly other metabolic products of the bacteria rapidly increase the permeability of the intestine Large quantities of toxin are absorbed and the sheep dies of acute enterotoxaemia

Experimental enterotoxaemia can be distinguished from death due to acidosis which can follow overeating on diets such as wheat

THE DIAGNOSIS OF ENTEROTOXAEMIA

It is sometimes claimed that it is difficult to make an accurate diagnosis of enterotoxaemia, or that the disease may be easily confused with other conditions It is true that it might be difficult to prove that a

sheep had died from enterotoxaemia, but with a reasonably fresh carcass it should not be difficult to establish a correct diagnosis beyond all reasonable doubt.

Apart from the post-mortem signs already described, the following criteria should be of value. The first is appearance of large numbers of organisms resembling *Cl. welchii* in the small intestine. In a fresh carcass of a sheep dead from some other condition no organisms of this type can be seen, and even in an animal long since dead the post-mortem invaders are usually of many species and do not give the same appearance as the mass of straight thick rods seen in typical enterotoxaemia (Bennetts, 1932; Bullen and Scarisbrick, 1957).

It is, of course, essential to demonstrate the presence of epsilon toxin in the intestine. The gut contents should be mixed with an equal volume of saline and centrifuged at high speed until the supernatant fluid is clear. The supernatant fluid should not be filtered through a Seitz EK pad which may adsorb considerable amounts of epsilon toxin. Properly clarified centrifuged material seldom contains substances that cause nonspecific deaths in mice. It is debatable whether it is worth while to estimate the concentration of the toxin present. The presence of only low concentrations in a carcass is no indication of the concentration in the intestine during life. Exact knowledge of the fate of epsilon toxin in the intact carcass is uncertain, but there is some evidence that there is a rapid decline immediately after death (Bullen and Scarisbrick, 1957). The toxin usually survives for a long time in the supernatant of centrifuged intestinal contents kept at $+4°$ C. It will keep indefinitely if frozen at $-20°$ C.

The urine should aways be examined for sugar. Even a few drops may be sufficient to give a positive reaction with Benedict's reagent. Glycosuria combined with the presence of epsilon toxin in the intestine strongly suggests enterotoxaemia, although it must be remembered that glycosuria can occur with other causes of death. If one or two ml. of urine give a negative reaction, then death is unlikely to be due to enterotoxaemia, as the absorption of a lethal dose of epsilon toxin invariably results in a hyperglycaemia.

The pulpy kidney lesion, though only a post-mortem change, is a useful sign provided the carcass is reasonably fresh. It is important to recognize the difference between ordinary post-mortem softening and the typical pulpy kidney lesion. Typical pulpy kidneys even in a carcass only 6–12 hours old are so soft that they can be squeezed through the fingers with ease.

Strong evidence in favour of a diagnosis of enterotoxaemia is suggested by the following (1) the characteristic microscopical appearance of organisms resembling *Cl welchii* in very large numbers in the intestine, (2) *Cl welchii* epsilon toxin in the intestine, (3) glycosuria, (4) the 'pulpy kidney' lesion The occurrence of glycosuria in natural cases of enterotoxaemia has recently been confirmed by Jansen (1960)

THE PREVENTION OF ENTEROTOXAEMIA

Management The close association between good feeding conditions and enterotoxaemia due to *Cl welchii* Type D has led a number of people to attempt to prevent or curtail outbreaks of the disease by restricting the food supply Unfortunately many of these attempts have not been done with suitable controls Nevertheless Gill (1933) thought that the 'yarding' of lambs for 24 hours every 5–7 days was of value Gill described 'yarding' as keeping the flock in a yard, without food from 6 a m to 6 a m the following day In one instance 434 lambs were divided into two equal groups One lot 'yarded' every 7 days had a death rate of 0 5 per cent The death rate in the controls was approximately 3 per cent Bennetts (1932) merely states that the preventive effect of grazing on scrub country was well known Newson and Cross (1943) state that deaths from 'overeating disease' may be stopped practically overnight by withholding grain Shaw, Muth and Seghetti (1939) mention that attempts made to control pulpy kidney disease in Oregon by Gill's method of yarding were apparently without success

Foggie and MacNab (1939) described some interesting results on the effect of *Cl welchii* Type D antiserum and the temporary starvation of lambs on the incidence of the disease 1,851 lambs from 20 farms were used for the experiment On each farm the lambs were divided into three groups, of approximately equal numbers One group were penned away from the ewes for a period of not less than 7 hours and in some cases the lambs were also docked and castrated The mortality in the control group was 2 4 per cent in those receiving antiserum 0 3 per cent and in those temporarily starved 0 4 per cent

There is thus strong circumstantial evidence that a temporary reduction in the food supply may help to prevent enterotoxaemia The fact that overeating and a change of diet were essential for the production of experimental enterotoxaemia also suggests that limitation of the food intake might help to prevent the development of the disease

Immunization. Adequate immunization against *Cl. welchii* epsilon toxin is the best method of protection against enterotoxaemia due to *Cl. welchii* Type D. Circulating epsilon antitoxin gives complete protection provided the concentration is sufficiently high. Bullen and Scarisbrick (1957) found it impossible to reproduce experimental enterotoxaemia in animals with high levels of circulating antitoxin, even when very high concentrations of toxin were maintained in the intestine for many hours on end.

Thomson and Batty (1953) suggested that the minimum level of circulating epsilon antitoxin required for adequate protection is 0·1 units per ml. of blood. Smith and Marsh (1953) state that 0·3 unit per ml. gives adequate protection and that lower amounts are probably sufficient. Montgomerie and Thomson (1954) describe three methods of immunization. (1) The passive protection of new-born lambs by the consumption of colostrum from an actively immunized ewe. The level of protection transmitted to the lamb will depend entirely on the amount of circulating antitoxin in the ewe. Colostrum from a well-immunized ewe should provide adequate protection for about four weeks. (2) Passive protection of lambs by injection of hyperimmune horse serum; 2 ml. in lambs and 5 ml. in sheep over 6 months old of suitable antitoxin will provide a circulating epsilon antitoxin level of >0·1 unit for about three weeks. (3) Vaccination with *Cl. welchii* epsilon toxoid. The response to toxoid depends upon the animal's previous experience of the antigen. If the sheep is sensitized to epsilon toxin and possesses even traces of circulating antitoxin then the response to a single dose of vaccine is usually good. On the other hand if the sheep are not sensitized to the epsilon antigen the injection of a single dose stimulates little or no antitoxin. This dose should however provide adequate sensitization so that a second injection of antigen 4–6 weeks later should provide a good response.

In Great Britain it is not uncommon to find flocks which have a certain level of natural immunity (Montgomerie and Thomson, 1954). This immunity can occur suddenly and is probably derived from the absorption of small amounts of epsilon toxin produced by *Cl. welchii* Type D present in the intestine (Bullen and Scarisbrick, 1957). In the case of valuable flocks it might well be worth while to bleed and test a number of animals to get some idea of the level of natural immunity before starting immunization.

Montgomerie and Thomson (1954) recommend the following programme of immunization in a flock in which the disease had

occurred both in adults and lambs The ewes should be vaccinated early in the autumn, and revaccinated during the winter A third vaccination should be given about two weeks before lambing begins to provide a high level of circulating antibody which will be transmitted to the lambs in the colostrum The lambs will be protected by the transmitted antibody for about 4–6 weeks and may be vaccinated within the first few days of life and revaccinated 6 weeks later to provide adequate protection for at least 6 months All the ewes should then be revaccinated about two weeks before any future lambing

Antigenic efficiency of Type D vaccines Batty and Glenny (1948) showed that the antigenic efficiency of *Cl welchii* Type D toxoid was increased by treatment with trypsin They found for example that rabbits immunized with trypsin-treated anaculture produced nearly 10 times as much antitoxin as rabbits immunized with untreated anaculture Similar results were obtained with guinea-pigs and horses Thomson and Batty (1953) showed that alum-precipitated trypsin-treated toxoid stimulated the production of higher levels of antitoxin in sheep than either anaculture, anaculture plus alum or untreated alum-precipitated toxoid They also found that alum-precipitated toxoid gave better results than anaculture alone Percival *et al* (1954) state that lambs receiving anaculture did not show lower antitoxin levels than those receiving alum-precipitated vaccine (presumably alum-precipitated anaculture) Similar results were obtained by Munoz *et al* (1955) Nevertheless it would appear that alum-precipitated trypsin-treated toxoid is probably the most efficient vaccine at present available

ENTEROTOXAEMIA CAUSED BY TYPE A

Rose and Edgar (1936) described a condition in sheep and calves which they called enterotoxaemia jaundice In the acute form of the disease observed in sheep, death occurred after a very short period of illness characterized by dullness rapid pulse and respiration and haemoglobinuria In the subacute and chronic forms the skin and mucous membranes became yellow in colour There was a persistent diarrhoea and considerable loss in condition In calves the chief symptoms were dullness inappetence and haemoglobinuria On post-mortem examination of a fresh carcass there was evidence of acute jaundice All the body tissues were a bright yellow or a dull biscuit

colour. The liver was friable and often severely jaundiced. The small intestine was almost empty, the contents thick and creamy; the caecum was often deeply congested. Examination of the blood showed a striking haemoglobinaemia with the red cell count sometimes as low as a million. Post-mortem changes occurred very rapidly. In both calves and sheep large numbers of organisms resembling *Cl. welchii* were seen in the small intestine although very large numbers of coli-form organisms were also present.

A toxic substance was found in the intestinal contents of a number of sheep dying of the disease. Unfortunately in the great majority of cases only *Cl. welchii* Type D serum was available for neutralization tests. This gave complete protection against the toxin. It was found possible, however, to test a number of filtrates from cases of the disease in calves. The toxic material was neutralized by *Cl. welchii* Type A serum, and thus in all probability contained *Cl. welchii* alpha toxin. In general the evidence would suggest that the animals died from an enterotoxaemia due to *Cl. welchii* Type A. Nevertheless a more convincing demonstration of the presence of *Cl. welchii* alpha toxin in the intestinal contents of cases of this kind is probably required, especially in view of the invariable presence of *Cl. welchii* Type A in the intestinal contents of normal sheep and calves.

A brief mention of a similar type of disease has been made by Quin (1954). Schofield (1955) reported a series of sudden deaths in calves which he believed to be due to enterotoxaemia due to the *welchii* Type A. Post-mortem examination showed acute congestion of the duodenum and jejunum; sometimes the intestinal contents were stained with blood. A substance toxic for mice on intravenous inoculation was found on three occasions, but unfortunately no neutralization tests were done and the nature of the toxic material remains uncertain.

ENTEROTOXAEMIA CAUSED BY TYPE B

The most common form of this disease occurs in lambs. Referred to as 'Lamb Dysentery' in Great Britain, *bloedpens* in South Africa, the disease has also been described in North America, Australia and New Zealand (Smith, 1957).

Cl. welchii Type B was first isolated by Gaiger and Dalling (1923) from ulcers of lambs dead of lamb dysentery. The disease is almost entirely confined to lambs under two weeks old (Dalling, 1926; Gaiger and Davies, 1949). Losses of 20–30 per cent can occur. In

the very acute form of the disease the lambs are usually found dead, but in the majority of cases, especially in animals up to 10 days old, death occurs in about three days Symptoms consist of severe abdominal pain and dysentery In a more chronic form of the disease the lambs die after showing persistent diarrhoea for several days Some may eventually recover but this is rare

On post-mortem examination the lambs dead from the very acute disease often show nothing but an acute inflammation of the small intestine A few small ulcers may be present These are 1–2 mm in diameter with a yellow necrotic centre surrounded by a zone of acute inflammation The intestinal contents are bloodstained If the lambs survive for a day or two the ulcers may be 1–2 cm in diameter There may also be a peritonitis with a number of adhesions between loops of the intestine

IMMUNIZATION AGAINST LAMB DYSENTERY

Mason, Dalling and Gordon (1937) were able to show that lambs could be passively immunized against *Cl welchii* Type B by suckling an immune ewe Their main conclusions were as follows

> (1) Ewes immune against lamb dysentery do not transmit antitoxin to the lamb through the placenta (2) At parturition the antitoxic titre of the colostrum of immune ewes is greater than that of the serum. (3) Antitoxin in the colostrum is absorbed by a newly-born lamb but not by a four-day-old lamb (4) The first colostrum contains more antitoxin per volume than at any later time, the first suck by a lamb is important in the transmission of antitoxin (5) Heterologous antitoxin fed to a lamb or contained in the mother's colostrum is absorbed by the newly born animal (6) Heterologous antitoxin injected subcutaneously is absorbed much more rapidly than when administered by mouth. (7) The administration of either homologous or heterologous 'L D' antitoxin to pregnant ewes a short time prior to lambing confers a definite protection to their lambs against naturally occurring lamb dysentery

The methods of immunization employed today are based upon this work Lambs can either be injected with a suitable dose of *Cl welchii* Type B antitoxin immediately after birth or the ewes are actively immunized with Type B toxoid before the lambing season Ewes require at least two injections of vaccine, one dose about five months before lambing, and the second about two weeks before lambing In all subsequent years the ewes are revaccinated about two weeks before

lambing. This procedure should provide adequate protection for the lambs during the first two weeks of life.

ENTEROTOXAEMIA IN FOALS AND CALVES CAUSED BY TYPE B

Enterotoxaemia caused by *Cl. welchii* Type B can also occur in foals. Montgomerie and Rowlands (1937) described one case in a three-week-old animal. There were symptoms of abdominal pain accompanied by severe diarrhoea. Post-mortem examination showed acute inflammation of the small intestine with ulceration in the mucous membrane. *Cl. welchii* Type B was isolated from one of the ulcers. Mason and Robinson (1938) describe two outbreaks of the disease. In one instance 7 of 43 foals died of dysentery; in the other 7 of 17 foals died. Symptoms were noticed within 48 hours of birth and death usually occurred within 24 hours. All the animals had severe dysentery. This was followed by weakness, coma and death. On post-mortem examination the only lesion found was acute inflammation of the small intestine together with numerous dark red areas up to 1 cm. in diameter which may have been the beginning of ulceration. *Cl. welchii* Type B was isolated from the intestinal contents.

Hepple (1952) has described a case of enterotoxaemia in a calf due to *Cl. welchii* Type B. The animal was one of several, aged 7–10 days, which developed severe diarrhoea. Deaths occurred in 1–4 days from the onset of symptoms and a few animals recovered. The post-mortem lesions in the animal examined included an acute enteritis with extensive necrosis of the mucous membranes. The lesions were most severe in the ileum. The intestinal contents were bloodstained and contained both β and ϵ toxin, although the epsilon toxin was apparently only demonstrated after the filtrate had been treated with trypsin. *Cl. welchii* Type B was isolated from the ileum contents and the necrotic lesions.

ENTEROTOXAEMIA DUE TO TYPE C

SHEEP AND LAMBS

Clostridium welchii Type C was first isolated by McEwen (1930) from sheep dead of 'struck'. This term is applied to a fatal disease of sheep first noticed in the Romney Marsh area. 'Struck' is characterized by a sudden, almost symptomless illness, and rapid death. When seen before death the animals appear dull and dejected, do not feed or ruminate and they appear to suffer from severe abdominal pain. There

is no diarrhoea and no nervous symptoms. McEwen gives a detailed description of the lesions of the disease, the main features of which are as follows. Post-mortem examination shortly after death shows an acute peritonitis and enteritis. The peritoneal cavity may contain up to three litres of pale yellow fluid, which is sometimes tinged with blood. There is intense congestion of the peritoneal vessels and numerous subperitoneal haemorrhages. Parts of the small intestine show moderate or acute congestion, frequently accompanied by ulceration of the mucous membrane. The ulcers vary from 2 to 3 mm. in diameter to extensive lesions some 6–12 cm. long and 1–2 cm. wide. The intestinal contents often contain blood. There are no muscle lesions. McEwen points out that if the carcass is left for more than 8 hours before examination a characteristic post-mortem change develops in the subcutaneous and muscular tissue; the muscles become moist, soft and discoloured and in some cases full of gas. The whole picture resembles acute gas gangrene infection but is in fact due to post-mortem invasion.

The disease affects adult animals. Losses vary from 5 to 15 per cent and its incidence is variable and is often found more frequently on some pastures than on others.

Brooks, Sterne and Warrack (1957) describe the strains originally isolated by McEwen as the 'classical' Type C.

Griner and Johnson (1954) described an acute fatal haemorrhagic enteritis in lambs in Colorado. The disease occurred some 12 to 72 hours after birth, and in one flock the incidence was high, 12–20 per cent of the lambs per day. There were no characteristic symptoms other than sudden death. The post-mortem lesions described are almost identical with those of 'struck': an acute peritonitis, patchy acute enteritis, with blood and desquamated necrotic mucous membrane in the intestinal contents.

ENTEROTOXAEMIA IN CALVES DUE TO TYPE C

Griner and Bracken (1953) described an acute haemorrhagic enteritis in calves in Colorado, the greatest loss occurring between the ages of 3 and 5 days. All the animals were in good condition before the disease appeared. The animals died suddenly, usually within 2–4 hours of becoming ill with signs of acute abdominal pain; occasionally blood-stained faeces were observed. On post-mortem examination the chief lesions consisted of an acute haemorrhagic enteritis of the jejunum and ileum with necrosis and desquamation of the mucosa.

The intestinal contents were bloodstained. The strains of *Cl. welchii* Type C from Colorado differ slightly from the 'classical' strain (Brooks, Sterne and Warrack, 1957).

ENTEROTOXAEMIA IN PIGLETS DUE TO TYPE C

Field and Gibson (1955) described a form of haemorrhagic enteritis in piglets. Deaths occurred between 30 and 72 hours of birth. Occasionally cases are observed up to 14 days of age. The loss in affected litters was severe, and appeared to vary from approximately 20 per cent to 100 per cent. Symptoms consisted of dullness and weakness. Some developed dysentery in the final stage of the disease. Post-mortem examination showed a haemorrhagic necrotic enteritis of the small intestine with blood-stained intestinal contents. Brooks, Sterne and Warrack (1957) showed that the *Cl. welchii* Type C strain from the piglets differed slightly from the 'classical' and Colorado strains.

All forms of enterotoxaemia caused by *Cl. welchii* Type C appear to be characterized by rapid death and extensive destruction of the mucous membrane of the intestine. The nature of the predisposing causes of the infection are uncertain. In calves and pigs the animals are usually receiving large amounts of milk and it might be postulated that this could provide a suitable substrate for rapid growth of *Cl. welchii* Type C. Nevertheless, McEwen states that losses from 'struck' are believed to be heaviest when pastures are short and grazing scanty. The disease has been reproduced with massive doses of culture and toxin, or culture alone (McEwen, 1930) but unfortunately the results of these experiments cannot very well suggest what the predisposing causes of the disease might be.

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CHAPTER TWENTY-THREE

Calcium and Phosphorus

JOHN T ABRAMS

Introduction—Nature of the problem—Distributions and functions of calcium and phosphorus in the animal body—Alimentary absorption of calcium and phosphorus, action of vitamin D, importance of dietary Ca/P ratios, mechanism of calcium and phosphorus absorption—Calcium and phosphorus content of herbage—Practical applications, the general situation of the grazing animal, calcium and phosphorus requirements of sheep and cattle, recognition of field deficiencies, the effects of dietary Ca/P imbalance—Conclusions

Calcium and phosphorus are two of the consort of twenty or so chemical elements which are necessary for the maintenance of life in the higher animals All are equally important and life ceases if any one of them is missing furthermore, they need to be provided continually in food in various, suitable proportions In addition calcium and phosphorus were two of the first members shown to have a closely related connection with each other, whilst it is within the last three or four decades that further interrelationships have been disclosed

THE NATURE OF THE PROBLEM

With the sole exception of oxygen, none of the elements necessary to life is found in living tissues *as an element*, although a number of them, of which calcium is one, occur as ions most, including calcium and phosphorus, are present in the living body as chemical compounds What baffled early students of the chemistry of life—and still remains a major problem in biochemistry—was the variety of compounds to be

found in any living organism. Indeed, the difficulty of separating and identifying the great variety of substances was of such magnitude that it was by-passed in favour of simplicity. If animal tissues are burned under suitable conditions, most of the compounds of carbon, hydrogen, oxygen and nitrogen are converted into volatile gases, whereas the other elements remain behind as ash, the weight of which is usually but a few per cent of the original weight of fresh tissue.

With elements reduced to that form the nineteenth-century chemist could tackle the problem, knowing that all of the original calcium would be present in the ash as calcium oxide, calcium carbonate or other simple calcium salt whilst the phosphorus would be there as salts of phosphoric acid. Thus arose the custom of reporting the amount of calcium in foodstuffs as calcium oxide, CaO, and the phosphorus as P_2O_5, instead of the weights of the elements themselves.

This crude method of analysis can be applied to parts of animals or plants, so that information may thus be gained about the distribution of the two elements in living organisms. By the repeated application of such a technique, the details of which are of no immediate concern, we now know something about (*a*) the distributions and general functions of calcium and phosphorus in the animal body; (*b*) the modes of absorption of the compounds of these elements from the alimentary canal; (*c*) the occurrence of such substances in plants, especially grasses and clovers, and (*d*) the *practical* implications of the subject-matter of the three preceding sections.

THE DISTRIBUTION AND FUNCTIONS OF CALCIUM AND PHOSPHORUS IN THE ANIMAL BODY

About 99 per cent of the total calcium of the animal body is present, but definitely *not* 'locked away', in the bones and teeth: by contrast about 30 per cent of the phosphorus is found in the soft tissues, even though it also is an important bone constituent.

In mammalian blood the level of calcium is kept fairly constant at about 10 mg. per 100 ml. If it does fall much below this level the process of blood clotting may be seriously impaired. Furthermore, although only about half of the total blood calcium is in ionic form, the remainder being bound to protein, calcium ions are necessary for the proper functioning of nerve and muscle. Again, the mammalian secretion of milk may be regarded as bone formation by proxy, since the dam has to provide the necessary nutrients, including calcium and

phosphorus, for the growth of sucklings in cow's milk calcium and phosphorus are each present to the amount of about 5 gm per gallon

Present evidence indicates that phosphorus is present in living cells as derivatives of orthophosphoric acid, $OP(OH)_3$ Thus the inorganic fraction of bone contains calcium and phosphate, which together help to form the crystal lattice of bone Furthermore, phosphorus occurs in some of the organic structural components of the body, as for example in the phospholipids More spectacular, in the light of the discoveries of the last three decades, but not more vital, is the part played by phosphate within the tissues both in the build-up of carbohydrates, fats and proteins and in their breakdown with consequent energy release

It was suggested earlier that calcium and phosphorus are not 'locked away' in the bones, they should indeed be looked upon as useful reserves upon which the organism can draw in time of need, a metabolic bank in fact but, like any normal bank, one from which it is not possible to make unlimited withdrawals During lactation, for example, dietary calcium or phosphorus intake at times may not suffice to cover the amount lost in the milk secreted, so whilst such a net loss to the lactating animal cannot continue indefinitely, the depletion of the calcium and phosphorus of the bones may serve a useful temporary purpose Replacement is to be expected and to be provided for during the dry period

Though it is important to the farmer, the lactating animal must not usurp all attention for bone growth in meat-yielding animals is also significant Apart from the wastage of adult beasts from dairy herds, meat is provided largely by young stock and it was shown many years ago by Hammond (recent summary, 1955) that the sequence of development in the growing beast is the vital organs, such as the brain and heart, followed by the bones, skeletal muscles, and subcutaneous and visceral fat Where the beast is adequately fed the different stages are crowded together if its nutrition is poor they are spread out in time The bony framework is thus a prerequisite to the healthy development of muscle, i e meat, so that no farmer, desiring to get his young stock quickly to marketable condition, can afford to neglect to provide for the growth of their bones he must therefore pay careful attention to the amounts of calcium and phosphorus in the feed of his beasts Where fattening at grass is his object, the composition of the herbage is thus important

THE ALIMENTARY ABSORPTION OF CALCIUM AND PHOSPHORUS

When, to Owen Glendower's boast, 'I can call Spirits from the vastie Deepe', Hotspur replied, 'But will they come, when you doe call for them?', he was providing a parallel for modern problems involving calcium and phosphorus. To know the rate at which bone grows in young sheep or cattle, or the output of the two elements in milk, is one thing: to call upon the diet to match these requirements is quite different. Indeed, it is a problem which has been responsible for a steady stream of research since the earlier part of the century, when Mellanby showed that rickets, the bone disease characteristic of the ill-fed, growing animal, could be produced at will in the young dog by suitable dietary manipulation. Later workers demonstrated a like position for the rat and the chick.

First, however, how does one determine how much calcium and phosphorus are needed daily for a growing calf, or lamb, or young pig? The initial thing to be settled is what we mean by a young calf, lamb or pig, for a lamb may be a lamb whether it takes four months or ten months to reach slaughter weight. Now, if the answer to this question does not rest entirely with the farmer and his customer it does so to a surprising degree. The former desires a beast that will grow to market weight quickly and cheaply. Aided by the nutritionist and a host of other specialists, he is able to do this nowadays in a way that would have surprised most farmers of fifty years ago: in the case of poultry growth rates are now fantastic compared with what they were even twenty years ago.

If, then, the animal is *first* defined in this manner (which may well change in another decade!)—there are two classical methods of deciding how much calcium and phosphorus are needed for the purpose. In the first of these a group of beasts, as nearly as possible alike in species, breed, age and weight, is divided into several groups, one of which is slaughtered immediately, the carcases being analysed for their contents of calcium and phosphorus, whilst the rest are then similarly housed and fed. At pre-determined intervals other groups of the animals are killed and treated just as the first group. In this way the gradual build-up of the two elements in the animal body can be followed and, knowing the time interval concerned, one can calculate their average daily rates of deposition for animals of selected ages. As an alternative to this method one may use a—usually—shorter type of test, in which

the calcium and phosphorus contents of the food consumed and of the corresponding excretions of faeces and urine are measured. That fraction of the intake which cannot be found in the excreta is deemed to rest in the body of the animal. There are slightly more modern versions of both of these techniques but they need no extended comment here. Finally, the calcium and phosphorus contents of a gallon of milk are fairly easy to determine. In any given case, then, provided this basic type of investigation has been carried out, there should be no difficulty is saying what are the *very least* amounts of the two elements which the daily diet must provide: one may supply more than this, but can expect nothing better than suboptimal results or even ultimate disaster if the intakes fall below such figures.

Supposing, however, that the two elements are provided in just the calculated amounts, can one assume that all is well? Unfortunately, no! If for example, these elements are provided in a single lump of fused calcium phosphate, hard, and slow to dissolve in the gastric juices, they may be carried through the digestive tract before solution has been accomplished, and such solution is a necessary prerequisite to absorption through the wall of the gut. If they are to be absorbed, calcium and phosphorus must either be present in solution in the food or in particles small enough to permit their dissolving in the digestive juices before the food passes through the small intestine (Matsushima, Dowe, Comar, Hansard and Visek, 1955). In plants, such as the grazing animal may encounter, the two elements appear chiefly to be in solution, but if it is deemed necessary to supply a mineral supplement to such beasts, then a coarse, 'floury' type of mineral mix is desirable.

As indicated earlier, however, calcium and phosphorus are not to be found in elementary form in nature, nor is the animal body adapted to dealing with all kinds of compounds. Calcium is best provided in the freely available calcium-protein complex of milk, or as a salt which will dissolve easily in the digestive fluids, e.g. well-ground limestone (calcium carbonate). By contrast phosphorus presents a more difficult problem, so that the supplements given to the grazing animal are usually provided either by ground bone, derived from the bones of animals recently slaughtered, or by 'rock phosphate', which is found in large mineral deposits in various parts of the world. In composition rock phosphate approximates to that of bone ash but, apart from its being ground to suitable size, it is often processed for two other, very different reasons. Firstly, it may contain too much of the toxic element fluorine for it to be fed safely to many classes of livestock.

processing mineral acid is therefore employed to remove the undesirable fluorine or to reduce its content to safe levels (Committee on Animal Nutrition 1955). Secondly, as explained below, it may contain too high a proportion of calcium in relation to its phosphorus content, so that chemical treatment is used also to produce what is commonly called di-calcium phosphate, $CaHPO_4$. In fact, orthophosphoric acid, H_3PO_4, contains in the molecule three atoms of hydrogen, replaceable by metals and may give rise to three different calcium salts, depending upon whether one, two or three atoms of hydrogen are displaced by calcium. Clearly there will be no difference in chemical composition between $CaHPO_4$ and an equimolecular mixture of $Ca_3(PO_4)_2$ and $Ca(H_2PO_4)_2$. In other words a product derived from rock phosphate by treatment with acid and showing a composition corresponding with $CaHPO_4$ may consist of nothing more than that substance or it may contain any proportions of $CaHPO_4$ with an appropriate mixture of $Ca(H_2PO_4)_2$ and unchanged $Ca_3(PO_4)_2$.

The reader may feel inclined to protest that this is a complicated argument which has little to do with grazing but, nevertheless, it is relevant to two very important issues, (*a*) the mode of assimilation of phosphorus compounds and (*b*) the occasional need to supplement the intake of some grazing animals with mineral mixes of which 'di-calcium phosphate' in various commercial grades is one. Thus, in kiln drying, the over-heating of $CaHPO_4$ gives rise to the calcium salt of pyrophosphoric acid, $Ca_2P_2O_7$, whilst any $Ca(H_2PO_4)_2$ may yield the calcium salt of metaphosphoric acid, $Ca(PO_3)_2$: experiment suggests that pyrophosphate and metaphosphate are both poorly absorbed from the alimentary tract (Barrentine, Maynard and Loosli, 1944; Wilcox, Carlson, Kohlmeyer and Gastler, 1955).

It is thus true that it may be difficult to match the needs of livestock for calcium and phosphorus with dietary supplies, for not only are there the complications mentioned above to be considered but another remains to be faced. In seeds, including cereal grains such as may be used to supplement pasture at times of diminished growth, there occurs phytic acid, a substance derived from inositol and orthophosphoric acid and giving rise to insoluble calcium salts: unless phytic acid is broken down into its components as a result of microbial action in the gut, its phosphorus is unavailable to the animal. Although there is evidence that a substantial proportion of the phytic acid of normal feeds is actually decomposed in the adult bovine digestive

tract (Reid, Franklin and Hallsworth, 1947, Mathur, 1953) this is not necessarily so in very young ruminants such as lambs

Quite clearly least difficulty is likely to be experienced when simple salts of calcium and orthophosphoric acid are provided for livestock, and in experimental work with laboratory animals it is usual to add a 'salt mixture' to the diet, the salts commonly including calcium carbonate and calcium, potassium, or sodium orthophosphates

THE ACTION OF VITAMIN D

Mellanby (1918) was the first to show quite clearly that it was not sufficient to have suitable calcium and phosphate salts in the diets of puppies unless certain fats were also fed, rickets developed just as surely as if there were a mineral deficiency Later investigation of this occurrence revealed the existence in such fats of what is now known as cholecalciferol (vitamin D_3) and proved also that the vitamin might be supplied either in food or might originate in the skin of a beast if it were irradiated in some suitable manner, especially by sunlight Forty years later the precise mode of action of the vitamin still eludes examination but it has been shown that one of its actions is to assist the absorption of calcium from the small intestine (Nicolaysen, 1937) At this stage a slight halt must be called to emphasize that *three* nutrients at least are thus interrelated in calcium absorption in the dog Now, therefore, we require to be careful in showing that what holds good for the canine species is true also of the grazing animal It will be realized that as the number of related variables increases, so the chances steadily diminish of the *simultaneous* manipulation of those variables in experiments performed on farm animals, other than poultry, for the simple reason that very large groups of beasts are then required such large groups are very expensive to buy, manage and feed In reviewing the literature there is thus the ever-present danger of assuming that a given dietary relationship found to hold good with one species, e g rats, applies equally well to all others, e g sheep and cattle In the writer's opinion there are many gaps in our knowledge of the calcium and phosphorus metabolism of farm animals Nevertheless, evidence has been brought to show that the alimentary absorption of calcium and phosphorus by calves may be increased manyfold if they are given vitamin D (Wallis, Palmer and Gullickson, 1935) correspondingly, calves which have no source of the vitamin soon show the swollen joints and lameness that are the outward signs of rickets There is

little doubt that this is a quite general type of relationship, although it is not necessarily equally easily demonstrable in all species.

There is a further complication, to which reference will later be essential, namely that it is not necessary to feed vitamin D simultaneously with calcium and phosphorus nor to have the animal irradiated then, since mammals and birds are capable of storing considerable amounts of the vitamin at times when their intake exceeds their needs. Such stores may be drawn upon later if the food then provides none of the vitamin, or if sunlight is absent or is lacking in potency.

THE IMPORTANCE OF DIETARY Ca/P RATIOS

Although absorption and utilization of calcium and phosphorus are greatest when the elements are provided in the diet in the form of orthophosphates and simple calcium salts, it is not sufficient to furnish them in haphazard quantities. In growing animals good bone formation depends initially upon the amounts both of calcium and phosphorus provided in the diet. Alternatively, one may say that it varies with *the ingested amount of either calcium or phosphorus and the* dietary Ca/P ratio: the two statements are equivalent, though they are often used in confusing fashion. Nevertheless, it may seem surprising that bone formation should depend upon the Ca/P ratio. If, for example, feeding trials under good conditions have shown that a lamb can deposit certain quantities of calcium and phosphorus daily in bone, it is obvious that unsatisfactory results will be obtained when *less* than those amounts are provided by the available food: it is far from obvious that an inferior growth of bone should result from the use of *more* than such quantities. Nevertheless, the consequences do tend to become more and more unsatisfactory as the relative amounts of calcium and phosphorus in the diet (i.e. the Ca/P ratio) deviate increasingly from a ratio of about 1·5 : 1. This has been demonstrated for the young of a number of avian and mammalian species and it appears to be of general application; it applies to the pig (Dunlop, 1935) and the rat, but there are differences between species as to the degree of imbalance that can be endured, the rat, for example, being very tolerant.

In order to try to correct a Ca/P imbalance one may (*a*) increase the amount of calcium or phosphorus in the diet to give a ratio of about 1·5 : 1, or (*b*) reduce the amount of either element to the same end, or (*c*) increase the vitamin D intake. One should remember, however, that whilst the free provision of the vitamin will help to remedy an

imbalance, or the effects of a small daily supply of calcium and phosphorus, neither vitamin D nor any other nutrient can transmute the elements absolute deficiencies of calcium or phosphorus cannot be made good by further provision of the vitamin

THE MECHANISM OF CALCIUM AND PHOSPHORUS ABSORPTION

In a brief chapter of this kind there is little purpose in attempting to deal with details of the mechanisms of calcium and phosphorus absorptions, particularly as they are far from completely understood, but it is perhaps necessary to mention one important aspect of balance experiments where calcium intake of the food is measured during a given period for which the urine and faeces, corresponding with that food, are also collected and examined for their calcium contents If 10 gm of calcium are fed and if 4 gm of the element are found in the faeces, it is natural to assume that 6 gm have been absorbed from the digestive tract Modern techniques show quite clearly, however, that the faecal calcium consists of two components, namely, that which has not been absorbed and the remainder which, at some time or other, has entered the body but has now left it once again (Comar, 1955) In the adult cow there is also a steady flow of phosphate passing from the body through the walls of the rumen into the ingesta contained in that organ in the calf more phosphate enters the small intestine in this way than passes into the rumen (Smith, Kleiber, Black and Lofgreen, 1956)

From what has been said already in this section, it should be clear that the absorption and utilization of calcium and phosphorus from the alimentary canal are far from simple processes Much of the literature of the subject deals with young animals only, since rickets is easily observed in such creatures, but rather similar findings with respect to the calcification of adult bone have been observed in older animals Thus, calcium absorption in the cow is improved when vitamin D is supplied failing that, demineralization of the skeleton to the point at which spontaneous fractures occur is likely (Wallis, 1938)

THE CALCIUM AND PHOSPHORUS CONTENTS OF HERBAGE

Although climatic conditions in Britain tend to restrict grazing to a limited portion of the year, the post-war emphasis on grass production has led to an increased use of dried grass, hay and grass silage during the winter months To that extent the problems of the grazing season proper carry over into the time when cattle are housed In other parts of the world, notably New Zealand, animals may be out at

grass virtually the whole year round. It is essential, therefore, to examine the literature concerning the calcium and phosphorus contents of herbage. The subject was usefully reviewed (Thompson, 1953) in a paper which includes several references to studies by Thomas and his collaborators at Newcastle.

As the result of agricultural policy in Britain, aimed at the general improvement of soil fertility and the production of greater weights of herbage with increased nutritive value, two practices have been greatly fostered during recent decades; they are (*a*) the increased liming of land and (*b*) the ploughing-in of permanent pasture in favour of ley production. The leys which have been favoured have been of a relatively simple type, in which leguminous plants have had an important place.

Expressed as a percentage of the dry weight of the plant, the mean calcium content of several legumes was found to be 1·69 per cent (Ca, not CaO), whilst the corresponding figure for grasses was 0·39 per cent: for phosphorus (P, not P_2O_5) the percentages were 0·38 and 0·21 respectively (Thomas, Thompson, Oyenuga and Armstrong, 1952). In each group a wide range of values was observed. Other data in the literature are in concordance with these figures.

The stage of growth of vegetation may also influence the composition of herbage which tends to maintain its content of calcium with increasing maturity, although phosphorus percentage declines during such ripening, when its changes follow closely the variations of protein content. Nevertheless, one should not stress the differential effects of age too much, since modern pasture management aims at the utilization of young herbage by the grazing animal, the vegetation being kept under control by intensive cropping. Likewise, the production of hay and silage from the modern ley is designed to exploit the gathering of young grasses and legumes and the production of leys from simple seed mixtures enables the herbage to be cut when all the plants are at roughly corresponding stages of growth, there being no need for one plant species to be seeding while the others have yet to flower. Lastly, the liming of land tends to raise the calcium content of the plants growing thereon, whilst favouring the calcium-rich legumes at the expense of the grasses.

Quite clearly it would be foolish to make dogmatic assertions regarding the calcium and phosphorus contents of herbage in a particular case and one must also make due allowance for the grazing habits of the animals influencing the issue, as in the selection of leaves,

rather than stems, by sheep (Meyer, Lofgreen and Hull, 1957) Nevertheless, if average values of 1 7 per cent for calcium and 0 4 per cent for phosphorus in legumes, with corresponding figures of 0 4 per cent and 0 2 per cent for grasses, are assumed, they will provide working limits sufficient to yield useful information about the inorganic intakes of various classes of farm animal

PRACTICAL APPLICATIONS

Under modern farming conditions it seems that the term 'grazing animal' applies so largely to cattle and sheep that there is little reason for considering other species within the confines of a single chapter That being so, the matter for discussion consists of two main divisions relating to meat-yielding animals, both cattle and sheep, and to the dairy cow respectively In each case it will be necessary to examine what pasture offers in relation to the needs of the animals

THE GENERAL SITUATION OF THE GRAZING ANIMAL

Under present-day conditions in Britain herbage is expected to provide a substantial portion of the total food requirements of cattle and sheep It affords calcium and phosphorus in amounts to be discussed below but yields little or no vitamin D, although the presence of an anti-rachitic factor in green fodder has been claimed (Raoul, Le Bouleh Baron, Bazier and Guerillot-Vinet 1956) On the other hand large amounts of carotene or pro-vitamin A, occur in such foods Apart from deliberate supplementation of the natural diet with some concentrated form of vitamin D, the animal s intake of that vitamin will be almost entirely dependent upon solar irradiation, a quantity which is far from easy to determine

Now observers in New Zealand and subsequently in Britain and Holland have produced evidence linking carotene with the anti-vitamin D activity of green feeds for lambs, although not all of the affecting variables may yet have been discovered (Grant 1955) It thus appears that *four* variables have now to be taken into account, calcium phosphorus vitamin D and carotene intakes the position being made more complicated by the ability of the body to store large amounts of the two vitamins and thus to influence calcium and phosphorus absorption and utilization at a later period Anyone who sets out to establish the calcium and phosphorus requirements of farm animals especially of cattle and sheep, should thus have the beasts' carotene and vitamin D status under good control By chance this

has not generally been the case, much of the work having been done before the significance of vitamin D was fully realized and long before the anti-vitamin D activity of carotene had been discovered. Many careful studies were made in the U.S.A., but without such control, and in latitudes and climatic conditions so different from those of Britain (Abrams, 1952*a*) that wholesale translation of the conclusions from that country to this is unjustifiable. An experiment with four variables, even though no more than two levels of each variable are used, requires at least 2^4, i.e. 16, animals, without allowing for any duplication of treatment: three nutrient levels raise the necessary number from 16 to 81. It would be dishonest to pretend that experiments with cattle and sheep had ever been done on anything approaching these lines; instead we have to base conclusions on fragmentary tests, chipped off, as it were, from the ideal block.

On the whole the rate of usage of vitamin D appears to depend upon the Ca/P ratio and the absolute amounts of the two elements in the diet. Wallis (1938), the only worker deliberately to deplete his adult cattle of their reserves of vitamin D before starting his experiment proper, noticed signs of deficiency after 2–4 months: this was in a sunny state of the U.S.A. much more likely to lead to the build-up of vitamin D reserves than in Britain. Calves become deficient in similar circumstances in the U.S.A. 1–3 months (Duncan and Huffman, 1936). American pigs show signs of depletion after about 4 months if they are white and after 2 months if they are black (Johnson and Palmer, 1939). In South Australia lambs begin to show signs of deficiency in about 2 months (Franklin and Reid, 1948). Even under conditions more favourable to the animal than are likely to be encountered in Britain, it appears that the vitamin D reserves accumulated by sheep, pigs and cattle under good conditions of insolation are sufficient only for about 3 months at most. To what extent the time varies with the calcium, phosphorus and carotene intakes, or carotene reserves, it is difficult to tell from the heterogeneous data available. At the end of the average British winter livestock may well be depleted

graphical and climatological conditions under which mountain sheep exist make it difficult though far from impossible, to provide mineral supplements by contrast the provision of calcium and phosphorus for lowland sheep is relatively simple Compared with cattle, sheep have the advantage of being out for most of the year gleaning what sunshine there may be during the winter months though it cannot compare with summer sunshine In addition, sheep are likely to consume a greater proportion of carotene-rich green fodder than cattle and less hay Hay through solar irradiation is also a source of vitamin D but, due again to climatic conditions and to the modern tendency to get hay baled and under cover as quickly as possible after the initial wilting it is not a potent one

With respect to the calcium and phosphorus requirements of sheep the Committee on Animal Nutrition of the U S National Research Council said (1949) that not all are agreed on the question of the requirements for calcium and phosphorus nor on the optimum calcium phosphorus ratio' They base their recommendations chiefly on U S South African and Australian work the application of which to British conditions is subject to reservations More recently (1957) they have suggested that fattening lambs of 60 to 100 lb live weight require daily intakes of 2 7 to 4 0 lb of air-dried food containing 2 9 to 3 1 gm of calcium and 2 6 to 2 8 gm of phosphorus—the dietary Ca/P ratio is thus close to unity

At 0 4 per cent calcium and 0 2 per cent of phosphorus the average data reported for grasses such dry-matter intakes would afford 4 8 to 7 2 gm of calcium and 2 4 to 3 6 gm of phosphorus the calcium intake being more than adequate but that of phosphorus remaining rather doubtful If data for legumes are considered then both calcium and phosphorus are adequately covered but at the expense of a Ca/P ratio of about 4 1 On the other hand data provided by Hignett (private communication) for local herbage include calcium contents of 0 5 to 0 6 per cent with phosphorus at 2 5 per cent so that low or marginal phosphorus intake may frequently be combined with Ca/P ratios of more than 2 1 The occurrence of rickets overt or subclinical in lambs on winter green feed is thus not difficult to understand Moreover it must be stressed that unsatisfactory weight gains rather than frank rickets have several times been reported To the farmer this is the more serious for whilst rickets and lameness in livestock should be recognized readily sub-optimal weight gains may well pass unobserved

Recognition of the needs of mountain sheep for calcium, phosphorus and vitamin D, in order to prevent leg deformities ('bent leg'), goes back nearly forty years (Elliot and Crichton, 1926) whereas the detection of ovine sub-clinical rickets on green winter feed is much more recent. In the selection of preventive measures it appears to be useless to provide calcium and phosphorus if the real cause of trouble is an inadequate provision of vitamin D, either orally or via insolation (Franklin and Reid, 1948). The writer's view is that vitamin D supplementation is worth the trial. It costs little and sufficient for three months is easily given in a single dose. Progressive farmers could well test its efficacy themselves by giving it to a section of their flocks and comparing the response of those animals with that of the untreated beasts. On the other hand vitamin D should not be used indiscriminately at high dosage rates.

Good lamb production depends primarily on a good-milking ewe and sufficient herbage. Lactation involves an appreciable production of calcium and phosphorus in milk but the marked influence of lactation on mineral metabolism in the ewe has had relatively little attention (Benzie, Boyne, Dalgarno, Duckworth and Hill, 1959). Studies of the effects of different calcium intakes by Cheviot ewes, for which 2·5 ml. of cod-liver oil per ewe provided the daily supply of vitamin D, have been made during pregnancy and lactation. During mid-pregnancy, late-pregnancy and mid-lactation the rations provided 2·0, 3·3 and 4·6 gm. respectively per day, against supposed needs of 2·7, 3·4 and 4·8 gm. For the three different groups the calcium intakes were 1·8, 4·7 and 7·6 gm. day, a given level being maintained throughout pregnancy and lactation. The serum calcium levels and the state of the bones appeared to show the inadequacy of the lowest calcium intake under these conditions whereas there was little to distinguish between the effects of the two higher levels, so that 5 gm. of calcium daily would seem to be sufficient. These animals were fed on concentrates: estimates based upon corresponding intakes of grass- or legume-hay show that there would be no doubt about the attainment of the necessary calcium input but that the phosphorus might not reach the higher levels mentioned above. Further studies of this kind are necessary.

recommendations of the relevant Committees on Animal Nutrition of the U S National Research Council (1958*a* and 1958*b*) provide bases for comparisons

For the normal growth of steers and heifers from 400 to 1,000 lb live weight, the suggested total dry-matter intakes range from 11 to 22 lb per day· correspondingly the calcium content of the feed should vary from 0 26 to 0 13 per cent and the phosphorus from 0 30 to 0 13 On such bases the total daily intakes of both elements would be fairly steady at 13–14 gm By contrast average British grass would afford 20 gm of calcium and 10 gm of phosphorus for the lightest beast in the range and 28 gm of calcium and 14 gm of phosphorus for the heaviest With leguminous feed the corresponding pairs of intakes would be approximately 80 gm and 20 gm, and 110 and 30 gm respectively On the whole, the impression is given of more than sufficient calcium with too little phosphorus As these are *average* figures quite clearly some animals might well receive much less phosphorus

Feeding trials with Hereford steers, beginning at eight months of age when the average weight was nearly 500 lb, were carried out with fixed phosphorus intakes of about 12 gm per day (U S Recommended levels) but with Ca/P ratios of 1 4, 4 4, 9 1 and 13 7 for four different groups of animals The tests lasted 140 days and were repeated the following year Although no vitamin D was fed to them, the steers were exposed to good (Nebraska) sunshine and were fed on hay and concentrates together with necessary supplements of ground limestone to supply the desired higher levels of calcium intake The two higher Ca/P ratios were associated with distinctly smaller average daily weight gains than the two lower ones but there were no suggestions of significant changes in the calcium and phosphate levels of the blood (Dowe, Matsushima and Arthaud, 1957) Thus the insidious effects of high Ca/P ratios again seem to be confirmed British herbage may be unlikely often to produce Ca/P above 4, but there would seem to be the distinct possibility of both the absolute phosphorus intake and the vitamin D supply falling below the levels encountered in this American work.

More recent work with dairy heifers (Colovos, Keener and Davis, 1958) has confirmed the original findings of Mollgaard and Throbeck (1941) that the addition of limestone to feeds may depress their digestibility In this instance a daily intake of approximately 40 gm of calcium led to such a general depression whereas one of 20 gm did not,

nor did the addition of 1 or 2 per cent of dicalcium phosphate to the feed. To quote from the original paper: 'these results further indicate a need for additional work on the different effects of different levels of calcium and phosphorus on feed utilization.'

We may turn now to an aspect of the problem first brought to light by Hignett and Hignett (1951) who examined the calcium and phosphorus intakes of about 800 dairy cows, widely distributed over Britain, where there appeared to be a history of *herd* infertility and where specific disease could not be found. Artificial insemination was used for such animals and herd infertility was defined in terms of an arbitrary proportion of animals being returned for a second or subsequent service: the period of observation covered the six winter months. After an analysis of the data these workers concluded that, below a certain level of phosphorus intake, increasingly higher Ca/P ratios were associated with rising infertility; above that level of phosphorus intake there was diminishing infertility. Moreover, the level of phosphorus intake apparently necessary for the maintenance of a 1,000 lb. cow under British conditions was suggested to be not less than 21 gm. per day, an appreciably higher figure than the (U.S.A.) standard.

To the present writer it seemed that one was dealing here with a case of three closely interrelated nutrients, namely calcium, phosphorus and vitamin D, and that, under British conditions, a relative lack of the vitamin might seem more likely than absolute deficiencies of phosphorus (Abrams 1952*b*). Subsequent re-analysis of their data by Hignett and Hignett (1953) tended to support such a view, the fertility of the cattle showing little relationship to calcium/phosphorus intakes during October and November but responding definitely during February–March, with December–January taking middle place. This is to be expected if the vitamin D reserves of the cattle were becoming exhausted during the period of winter housing. Although this does not constitute positive proof, the sequence of events is in keeping with what is known about the rate of usage of reserves of vitamin D.

Similar findings of Hignett with respect to much smaller groups of heifers have been questioned (Littlejohn and Lewis, 1960), though on the basis of an equally small experiment, but no one has yet repeated his extensive trial with older animals under comparable circumstances. It may be pertinent that Wallis (1938) said, concerning his vitamin D-deficient cows; 'the breeding records are available for these animals for at least two lactations previous to the experiment. The regularity

shown by these records stands out in striking contrast to the fact that none of these cows showed estrum during the period of vitamin D deficiency' Wallis was unwilling, however, to say whether the response was a direct or an indirect one

THE RECOGNITION OF FIELD DEFICIENCIES OF CALCIUM, PHOSPHORUS AND VITAMIN D

Clearly, calcium and phosphorus may be present in food in such small amounts that they are not sufficient for the end in view (*absolute* deficiency) or they may be unavailable to the organism, though present in the fodder because for example, insufficient vitamin D has been provided (*conditioned* deficiency) In older studies the results of deficiencies stood out clearly in the form of dying animals, those with obviously deformed joints and those with disturbed blood levels of calcium and phosphate Deficiencies so marked ate now largely avoided, leaving the more difficult problem of the insidious effects of prolonged but mild deficiencies to be faced

THE EFFECTS OF A DIETARY Ca/P IMBALANCE

Recent as well as older studies have shown some of the more interesting sequels of dietary Ca/P imbalances though in many instances the precise mechanisms involved are not known Thus the addition of limestone to the diet of mice can result in the appearance of anaemia in the experimental animals the general interrelationships of iron, calcium and phosphate have been discussed by Greig (1952) Certainly mice are not 'farm animals' but the possibility that high dietary calcium intakes may lead to anaemia in brood sows apparently cannot be quite ruled out (Lucas, 1956)

Furthermore, the presence of too much calcium in the ration of the *dry-fed* bacon pig can give rise to a form of skin disease, parakeratosis, irritating to the animal and usually accompanied by poor food conversion rates if the same food is given *wet*, the condition does not arise (Thomas and Eden, 1954) When about 50 parts per million of zinc (e g as zinc carbonate) are added to it, the feed may then be given in dry form without the appearance of parakeratosis Alternatively, a reduction of the calcium content of the feed, without the addition of zinc, also prevents or cures the condition To explain this state of affairs it has been suggested that too high a dietary calcium content leads to the production of too great amounts of insoluble calcium salts in the small intestine and that zinc may be retained ('adsorbed')

with this insoluble material until it is excreted in the faeces; where there is a better supply of fluid, as in wet feeding, it is presumed that less zinc is lost from solution in this way (Lewis, Grummer and Hoekstra, 1957). In theory, such a reaction might well involve other trace elements in the diet.

In milk fever, which tends to occur at parturition in older cows, especially of certain breeds, it is possible that some dysfunction of the parathyroid glands occurs, as was first suggested by Dryerre and Greig (1925). On account of this dysfunction there is failure to mobilize the calcium reserves of the body at the beginning of lactation, with its call for 5 gm. each of calcium and phosphorus per gallon of milk. Consequently, blood calcium levels fall and the animal suffers collapse. How the parathyroid glands are 'put out of action' has never been properly explained, although it has been suggested that the provision and absorption of too much dietary calcium may lead to their atrophy. On this kind of basis attempts to stimulate the parathyroids to activity during the month or two preceding parturition have been made by feeding low calcium (*ca.* 10 gm./day), high phosphorus (*ca.* 100 gm./day) diets (Boda and Cole, 1956). An apparent reduction in the incidence of milk fever has resulted. Reports in confirmation of these views have been obtained from European sources (Ender, Dishington and Helgebostad, 1956).

Duncan (1958) has reviewed the problem of calcium/phosphorus balance in ruminants, keeping closely to those terms of reference and not deviating, as the present writer thinks is necessary, to take into account the vitamin D, or carotenoid, status of the animals. It will suffice here to quote from her opening paragraph; 'But when I began to study the material critically many gaps in fundamental knowledge appeared, and what seems a great discrepancy.' The discrepancy is between the results obtained by the two methods of determining calcium and phosphorus balances referred to in earlier paragraphs of this chapter. One of her conclusions is that further studies need to be made.

Work with radio-isotopes has suggested that two things may be markedly influenced by the Ca/P ratio of the feed of cattle. One of these is the size of the 'metabolic pool' of calcium. It has already been indicated that the calcium of bone is not just an inert mass, and such work supports the view that with low-calcium diets some 60 per cent of the total calcium of the body can be regarded as mobile and interchangeable, whereas with high-calcium intake it is only 36 per cent.

On the other hand the rate of turn-over or mobilization, of the calcium, as distinct from the amount available, varies in the opposite way with low and high-calcium diets respectively (Luick, Boda and Kleiber, 1957)

CONCLUSIONS

If this chapter had been a comprehensive account of calcium and phosphorus as they affect the grazing animal, it would have needed to be several hundred pages long Instead it is selective and represents the view of the writer, though not, it is hoped, a view that is inconsistent with the evidence

Nothing is easier than to criticize the work of other people If, however, the opinion is expressed (Abrams, 1952*b*) that many of the previous studies of calcium and phosphorus metabolism in grazing animals need to be repeated and very much extended, it is not to decry the work of able men, for their studies were made twenty, thirty or forty years ago Moreover, if it is now possible to comprehend the size of the task to be faced, much of our comprehension of the scope of the problem rests on their results even when they conflict one with another

Many millions of pounds are invested in the British dairy industry which is important to the whole nation, and yet if one were to be asked what is known with certainty concerning the calcium and phosphorus metabolism of the dairy cow, it is only a slight exaggeration to say simply that a gallon of milk contains about 5 gm each of calcium and phosphorus The claim that the cow at the height of lactation is inevitably in negative calcium and phosphorus balance, absorbing less of these elements than she excretes regardless of dietary intake, is one which is widely held, it is one that the writer does not feel justified by the nature of the evidence put forward

Science, at the low political level of the grazing animal, is doubtless international in its scope and freedom climate and farming methods are not There is ample evidence to suggest that our problems differ materially from those of the U S A just as they resemble in many ways those of Western Europe Moreover, in the past many of the experiments made to investigate mineral metabolism in farm animals especially cattle, have smacked of expediency, being tied too closely in scope, design and thought to contemporary modes of farming Rather than leading the farmer, they do not keep pace with the advances of which he is capable when he follows the precepts of other divisions of

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cattle, but in 1955 Blaxter and Sharman demonstrated hypomagnesaemia in milk-fed beef calves showing marked excitability and muscular convulsions under conditions when lead poisoning could be eliminated.

In sheep, although low serum magnesium concentrations have been observed for many years, the condition is thought to be analogous to the seasonal hypomagnesaemia without clinical signs (*vide infra*) often seen in cattle. However, subsequently, several workers (Stewart, 1954; Pook, 1955; and Penny and Arnold, 1955) have recorded the acute condition on either hill or lowland pastures or both.

OCCURRENCE

Hypomagnesaemia has been observed in most European countries, in New Zealand and also in parts of North America and Australia. It appears to be a disease associated with temperate climate since there is little reliable information with regard to its occurrence in tropical countries. According to Allcroft (1954) it is comparatively rare in Jersey cattle in the Channel Islands; this may result from the form of husbandry practised there.

INCIDENCE

Its incidence would appear to be on the increase, partly as a result of better facilities for diagnosis but, more important, as a consequence of the intensification of modern farming practice. Recent surveys (Withers, 1955, 1959; Grunsell and Paver, 1955) have suggested that the incidence of hypomagnesaemia in cattle in the United Kingdom amounts to almost 1–5 per 1,000 at risk, which is rather less than the 1–2 per cent noted by Seekles (1958) in Holland. Although the overall incidence for the United Kingdom suggests a disease of no great national significance, it does not necessarily give an accurate picture of its significance on the individual farm where very high economic losses may be encountered on occasion, as a result of the high mortality rate.

All breeds of cattle may be affected but the incidence, as assessed in a national survey of dairy herds, is five times higher in Ayrshire than in other breeds; in addition, the overall incidence is greater in Scotland than in England (Leech *et al.*, 1960). Both Sjollema (1932) and Blaxter and McGill (1956) have stressed the relationship between increase in susceptibility to hypomagnesaemia and age of the animal. Blaxter and McGill (1956) calculated that old cows which had had more than 6 calves were more than 14 times more likely to develop the

disease than were heifers in their first lactation. As a result of improved methods of control of tuberculosis, contagious abortion and mastitis, the average age of the cattle population in this country has increased. This increase in average age may be in part responsible for the apparent increase in the incidence of hypomagnesaemia in cattle.

The incidence of hypomagnesaemia in ewes, especially those transferred from rough to improved pastures in the spring, also appears to be on the increase (Hughes, 1958, Hughes and Kershaw, 1958). It occurs most frequently between 1 and 4 weeks after lambing when the milk yield reaches its peak, sheep with twin lambs being more susceptible.

It is important to note that, although only individual animals may show clinical signs, some degree of hypomagnesaemia may be present throughout the herd or flock, even though the animals therein may all be of about the same age. Thus variation in individual susceptibility must be implied. In addition to this, certain stress factors, such as oestrus, may be affecting only *certain animals during* the period of risk. Inglis, Weipers and Pearce (1959) noted that ewes with single lambs, twins and triplets showed progressively lower blood magnesium levels and certain sheep always tended to have serum magnesium concentrations higher than the flock average whilst certain others were consistently lower.

Outbreaks of the disease may be encountered at all times of the year, but it is usually accepted that such outbreaks are most likely to occur when dairy cattle are first turned on to a spring or autumn flush of improved grass. However, the disease is by no means confined to these periods and, in beef cattle in particular, cases have been reported which have occurred under both stall-fed and outwintered conditions during the winter months (Allcroft, 1947b).

may exist between the convulsive attacks during which time great care is necessary in handling these animals since unexpected noises or the prick of a needle may precipitate a fatal series of convulsions. In chronic form there is a gradual loss of condition but not always accompanied by a loss of appetite and decrease in milk yield. The condition may last for weeks and then may either resolve gradually or the acute phase may intervene, depending on circumstances. The chronic form of the disease was seen in Norway during the Second World War (Breirem *et al.*, 1954); it was considered to be caused by a diet low in calories and deficient in magnesium. In the United Kingdom it may be seen in outwintered cattle where the plane of nutrition is low (Allcroft and Green, 1938). In such animals it is possible to find levels of serum magnesium concentration with minimal clinical involvement which in the acute form would cause their death. It would appear that the neuromuscular junction, at which site hypomagnesaemia is thought to manifest itself, is able to adjust itself to a gradual fall in serum magnesium concentration without the production of hyperaesthesia. Only in the acute cases is the injection of a single dose of magnesium salts beneficial; in the chronic case, a temporary response is produced followed, about 24 hours later, by a return of the previous subnormal level.

The chronic form can be transformed into the acute form through the operation of a number of so-called 'trigger factors', the more important of which are oestrus and a sudden fall in environmental temperature coupled with exposure to bad weather.

In milk-fed calves the development of hypomagnesaemia is gradual so that the degree of hypomagnesaemia achieved is usually greater than in the adult acute form (Blaxter and Rook, 1954). In addition, the latent period, during which the conditions which predispose to hypomagnesaemia are present but clinical signs are absent, is a matter of months. This is a result of the relatively large store of readily available magnesium in the skeleton of the calf. It is seldom seen in calves under 6 weeks for two reasons: first, the presence of depletable skeletal reserve of magnesium; second, in older calves the large intestine ceases to be a site of magnesium absorption, so that there occurs a progressive decrease with age in the ability of the calf to utilize dietary magnesium. This continues until the range of magnesium availability normally observed in adult cattle is reached (Smith, 1959). The animals which are most prone are those with a rapid rate of growth and thus a relatively greater demand for magnesium. The disease is virtually impossible

to diagnose with certainty at a post-mortem examination, though the finding of a raised calcium-to-magnesium ratio in bone from a calf may be accepted as diagnostic evidence

of prophylactic dietary magnesium supplementation either directly the animal or indirectly via the herbage after fertilizer application the pasture. Also, in a comprehensive series of grazing experimen Kemp *et al.* (1960) demonstrated a significant positive correlation b tween the magnesium content of herbage and the serum magnesiu concentration of lactating cows. They showed that low seru magnesium levels did not occur when the herbage magnesium conte was higher than 0·20 per cent Mg, on a dry-matter basis. Howeve low serum magnesium concentrations were not invariably associat with the ingestion of herbage containing less than 0·20 per cent Mg.

The paradox can be resolved only through the realization that the is no simple aetiology to the disease but that a combination of facto are involved, some of which involve the pasture, some the animal an some the overall management. Basically six variables are concerne

(1) the size of the labile, or depletable, pool of magnesium withi the animal,
(2) the extent of obligatory excretion from the pool,
(3) the efficacy of absorption, or availability, of the dietary magne sium,
(4) the magnesium composition of the feed,
(5) the weight of feed consumed,
(6) the demands of production (pregnancy, lactation and growth and of stress.

Stress factors include oestrus, an increase in metabolic rate associate with inclement weather, and so on.

LABILE MAGNESIUM

Until the advent of a suitable radio-isotope of magnesium, Mg^{28} the extent of the freely exchangeable magnesium in an animal wa impossible to assess. With the aid of this isotope, Care (1960*b*) showed that the 24-hour exchangeable magnesium of a sheep amounted to 60 mg. per kg. body weight. It included not only all the extracellular fluid magnesium but also some of the intracellular magnesium. However, this exchangeable intracellular magnesium was small relative to the weight of the total intracellular magnesium. In addition, he suggested that the reserve of labile or depletable magnesium was even smaller and only amounted to 11 mg. per kg. body weight. These conclusions supported Cunningham's findings (1936*b* and *c*) that the bone and soft tissues from adult hypomagnesaemic animals

had virtually the same magnesium content as those from normal animals Blaxter and McGill (1956) confirmed that most of the magnesium in a normal adult animal was not readily exchangeable, and Field (1960) demonstrated with Mg^{28} that the fraction of bone magnesium *in* equilibrium with the magnesium of the body fluids after ten hours was only about 2 per cent

Recent work by MacIntyre (1959) using Mg^{28} has served to modify this concept somewhat He showed that the magnesium in many tissues could be exchanged in part for Mg^{28}, although actual depletion of muscle magnesium took 9 weeks to produce in rats (MacIntyre and Davidsson, 1958) However the important point is that most of the magnesium of the adult body although exchangeable with varying degrees of rapidity, is not quickly depletable to a marked degree under conditions of sudden magnesium deficiency

In the very young animal, on the other hand the skeletal reserves of magnesium are largely in an available state Blaxter and Sharman (1955) showed that calves fed a milk diet deficient in magnesium gradually lost 60 per cent of their bone magnesium as the plasma magnesium concentration decreased It is thought that as bone becomes less vascular with advancing maturity so the bone magnesium becomes less labile

OBLIGATORY EXCRETION OF MAGNESIUM

It appears that the adult animal has little reserve of magnesium readily available to it in time of need but is dependent upon the maintenance of a satisfactory level of dietary magnesium absorption to counter the obligatory excretion of magnesium, which takes place into the alimentary tract, and also to satisfy any requirement for production Urinary loss of magnesium may be disregarded under conditions of low magnesium intake when the plasma magnesium concentration falls below the renal threshhold Urinary excretion is thought to represent the major route by which excess absorbed magnesium is removed If the growth rate is zero and there are no demands of lactation or gestation, the endogenous faecal loss of magnesium represents the debit against which magnesium absorption must be credited Under normal conditions the endogenous faecal magnesium excretion by sheep has been estimated with the aid of Mg^{28} (Field, 1959, MacDonald, Care and Nolan, 1959, Care, 1960*b*) and was found to be of the order of 2–5 mg per kilo live weight. It usually exceeded the corresponding urinary excretion. However, little evidence is available regarding

this endogenous excretion under hypomagnesaemic conditions. Assuming that it remains appreciably unchanged an adult sheep would have to absorb about 200 mg. magnesium daily to maintain this loss, irrespective of any production requirements. This represents a relatively large proportion of the labile magnesium reserve for sheep of this size (which would have a reserve of 600–700 mg. labile magnesium). When hay was fed to normal sheep the true availability of the dietary magnesium was found to be about 25 per cent measured with the aid of Mg^{28} (Field, 1959; MacDonald *et al.*, 1959). This means that the minimal dietary intake for such a nonproductive sheep under these conditions would be 800 mg. magnesium daily or, by analogy on a body-weight basis, a comparable cow would require about 8 gm. dietary magnesium each day. This confirms the findings of Carberry, Chatterjee and Talapatra (1937) that magnesium intakes in oxen of about 9 gm. daily usually led to positive magnesium balances. When lactating, each gallon of milk produced will contain approximately 0·6 gm. magnesium for which about 2·4 gm. dietary magnesium will be required, assuming the availability of the dietary magnesium to remain at 25 per cent. Thus, for maintenance and the production of three gallons of milk the daily requirement of magnesium at this percentage availability amounts to 15·2 gm. magnesium. With this magnesium intake it should be possible, in theory, to maintain the plasma magnesium concentration at the level of the renal threshhold if the percentage availability of the magnesium does not fall below 25 per cent. Since the dry-matter intake of such a cow could be taken to be 30 lb. daily, the critical dietary magnesium concentration on a dry-matter basis would be about 0·11 gm. Mg per cent. Kemp *et al.* (1960) have demonstrated that low serum magnesium levels did not occur when the dietary magnesium concentration was higher than 0·2 gm. Mg per cent on a dry-matter basis. This suggests that either the percentage availability of magnesium under conditions associated with hypomagnesaemia falls to less than 25 per cent or the dry-matter intake falls. A fall in apparent availability and also in total magnesium was noted by Rook, Balch and Line (1958) and Rook and Balch (1958) when cows were transferred abruptly from a winter ration to spring herbage; this dietary change was accompanied by a progressive development of hypomagnesaemia. Similar findings for availability have been obtained with sheep (Care and Ross, 1960), but not by Field, McCallum and Butler (1958).

It would thus seem advisable to aim for a herbage magnesium level

of 0·2 mg Mg per cent as a prophylaxis against hypomagnesaemia and to regard any grass of inferior magnesium content with suspicion

THE AVAILABILITY OF DIETARY MAGNESIUM

True availability is the percentage of ingested magnesium absorbed from the alimentary tract It is given by (I − F + E)100/I, where I is the daily intake of magnesium, F is the total faecal output of magnesium and E is the endogenous faecal excretion of magnesium True availability can only be measured accurately by the use of a suitable isotopic tracer

Apparent availability, or (I − F)100/I, is obtained by the orthodox balance techniques

Since apparent availability does not take into account the endogenous excretion of faecal magnesium it is possible that the fall in apparent availability associated with the sudden change from a dry ration to a lush pasture may be indicative of increased endogenous faecal excretion of magnesium or decreased absorption of magnesium or a combination of the two Apparent availability of magnesium varies widely for different diets, even typical winter rations showing a range of 10–40 per cent (Rook and Balch, 1958) Moreover, it appears to be related to the magnesium concentration in the diet in such a way that the percentage availability rises in a non-linear manner as the magnesium concentration falls (Graham, Caesar and Burgen, 1960) The mechanism by which the efficiency of magnesium absorption is regulated remains unknown, in fact, a full understanding of it would be likely to reveal the key to the solution of the problem of hypomagnesaemia. The existence of marked individual variation in magnesium availability implies differences in the efficiency of utilization of dietary magnesium and may account to some extent for the different susceptibility to hypomagnesaemia often observed in members of the same flock or herd This must be taken into account when recommending dietary allowances of magnesium

The effect of the heavy fertilizer treatment of pasture with nitrogen and potassium on the incidence of hypomagnesaemia is well known (*vide infra*), but the extent to which this is due to the reduced magnesium intake or to the reduction in availability remains to be determined. It is possible that the mechanism which relates the percentage magnesium absorption to the magnesium intake may be affected by the pasture fertilizer treatment. This may occur in such a way that a decrease

rather than an increase in magnesium availability takes place following a reduction in the dietary magnesium intake.

Vitamin D does not appear to promote the absorption of magnesium from the alimentary tract of ruminants (Smith, 1958; Heath and Allcroft, 1960) as it does in the case of calcium. However, there does seem to be some interrelationship between calcium and magnesium absorption, and Alcock and MacIntyre (1960) have postulated the existence of a common transport mechanism for these two ions from the alimentary tract of rats. Thus, on a calcium-deficient diet magnesium absorption is increased, and vice versa. These results can explain the increased requirement of calcined magnesite fertilizer in a limestone or chalk area to prevent the incidence of hypomagnesaemia.

THE DIETARY INTAKE OF MAGNESIUM

Since magnesium is an essential element for plants as well as for animals, data on the mineral composition of individual herbage and crop plants are plentiful in the literature. The average content of some cattle feeds is given in Table 24.1 (Blaxter and McGill, 1956); the range of individual variability is very high and these figures are meant to indicate trends rather than absolute values.

From this table it can be seen that magnesium, unlike calcium, tends to accumulate in seeds, particularly oil-bearing seeds, and to be low in leaves, where calcium is usually high. Legumes and herbs are particularly rich in magnesium. It should be pointed out that there is a definite seasonal variation in the magnesium content of herbage with a minimum around April–June (Reith, 1954).

Little work has been done to determine the forms in which magnesium exists in plants. It is possible that some may be bound in such a way as to be almost unavailable to the animal whereas the converse may also hold true. Thus, it is possible that pasture magnesium analysis alone may not present a true picture of the situation. In southern Germany and Switzerland, where pastures are also heavily fertilized with nitrogen and potassium, hypomagnesaemia is almost unknown. This may be due to the high proportion of herbs often present in their swards.

Animals turned on to lush spring grass obtain much less magnesium from a predominantly grass sward than they do later on, since the magnesium content of such grass is likely to be as low as 0·12 per cent Mg. However, as mentioned previously, even this comparatively low magnesium content should be sufficient to supply the magnesium

TABLE 24.1 *The magnesium content of some cattle foods*

	Mg content on dry basis %
Oil seeds and their products	
Linseed cake	0·48
Palm kernel cake	0·27
Proprietary concentrates	0·36
Cereal grains and cereal products	
Whole oats	0·09
Whole wheat	0·13
Whole maize	0·12
White rice	0·03
Wheat bran	0·51
Maize gluten feed	0·02
Wheat germ	0·34
Animal products	
Dried blood	0·02
Dried meat	0·03
Straws and hays	
Oat straw	0·10
Legume hays	0·30–0·60
Grass hays	0·15–0·30
Pasture grasses and herbage	
Clovers	0·69
Grasses	0·24
Herbs	0·75

requirements of a lactating cow assuming the dry-matter intake to be adequate and the availability of the magnesium to remain undiminished. These two provisions would seem to account for the disparity of opinion between those who consider there is no correlation between herbage magnesium composition and hypomagnesaemia and those who believe such a correlation exists. It was to account for any decrease in intake of dry matter and in magnesium availability that Kemp *et al.* (1960) have advocated that 0·2 per cent magnesium should be considered the *minimum* permissible level of herbage magnesium. At a normal dry matter intake and magnesium availability this would provide a lactating cow with about 27 gm. magnesium daily or about 12 gm. in excess of the theoretical requirement.

Pasture magnesium composition may be profoundly altered by suitable fertilizer treatment. Also in a soil low in exchangeable magnesium, plant magnesium uptake is likely to be restricted. The presence of excessive amounts of potassium in a soil, particularly when accompanied by high nitrogen treatment, increases the potassium content of grasses at the expense of divalent elements such as magnesium, the effect being greatest in grasses. In addition, the position is aggravated by the nitrogen used to produce an 'early bite', since this pasture consists almost exclusively of the grass component of the sward and is low in magnesium.

Heavy simultaneous fertilizer treatment with nitrogen and potassium increases the incidence of hypomagnesaemia. This has been well substantiated (Bartlett *et al.*, 1954; 't Hart and Kemp, 1956; Smyth, Conway and Walsh, 1958). Its effect is considered to be exerted by means of a combination of reduced magnesium intake and reduced availability of magnesium, although the way in which the availability is reduced remains unknown. In cases of wheat pasture poisoning in the United States the wheat pasture was shown to be low in magnesium and high in potassium and nitrogen (Fontenot *et al.*, 1960). Attention was focused by Head and Rook (1957) on the formation of ammonia in the rumen following the fermentation of protein and other nitrogenous compounds from the grass. They noted a threefold increase in the ammonia content of rumen liquor on changing the diet of cows from hay and concentrates to grass. This increase was accompanied by the appearance of small amounts of ammonia in the peripheral blood. They also found that when there was a hypomagnesaemic response to nitrogenous fertilizers, this was most severe in those animals having the highest levels of blood ammonia and urea. They concluded that the hypomagnesaemia and the concomitant fall in the urinary excretion of magnesium observed in animals turned on to spring pasture were due to a fall in the availability of the dietary magnesium associated with a high ruminal ammonia content. Magnesium is not usually absorbed from the rumen to any significant extent; the major absorptive site is thought to be the small intestine (Care and Hill, 1960). It is possible that this fall in availability may be brought about by a decrease in the proportion of ultra-filtrable, or ionic magnesium in the small intestine, a result of the high concentration of ammonia in the rumen.

Dutch workers (Brouwer, 1952; Kemp and 't Hart, 1957) favour a high herbage-potassium level as the prime cause of hypomagnesaemia

and Brouwer (1952) implicates an abnormal herbage anion-cation balance in particular

Kemp and 't Hart (1957) observed that the herbage from pastures on which cases of hypomagnesaemia occurred was on the average higher in potassium (K), phosphorus and chlorine but lower in calcium (Ca), sodium and magnesium (Mg) After a survey of the incidence of hypomagnesaemia in 15,000 milking cows they concluded that if the ratio of herbage K/(Ca+Mg) (all expressed in milliequivalents) is greater than 1 5, cases of hypomagnesaemia will occur and if it rises to 3 0, a 20 per cent incidence can be anticipated No significant correlation was found between the incidence of hypomagnesaemia and herbage concentrations of crude protein, phosphorus, chlorine and sulphur, and the effect of sodium was not clear It has been suggested that a relative sodium depletion might act as a contributory factor towards the onset of hypomagnesaemia There is some evidence that in sheep the mechanism may involve the adrenal cortex (Care and Ross, 1960) but in rats Ross (1961) has shown that the absorption of magnesium from the small intestine *in vitro* is dependent in a linear fashion on the sodium concentration present On the other hand, when Kemp (1959) increased the sodium content of a highly fertilized spring pasture by top-dressing it with Chilean nitrate, he did not prevent hypomagnesaemia in cattle grazing that pasture This conflicting evidence serves to show the prevailing lack of knowledge of the factors which affect the absorption of magnesium Although the effect of potassium appears clearcut, the role played by sodium remains obscure

Kemp and 't Hart (1957) also found a significant correlation between the incidence of hypomagnesaemia and temperature They showed that the potassium content of herbage was markedly affected by temperature fluctuations in such a way that a rise in temperature increased the potassium level and a fall decreased it As pasture calcium and magnesium contents were not much affected, the overall effect of a rise in temperature was an increase in the ratio of K/(Ca+Mg) in the pasture and thus an increase in the incidence of hypomagnesaemia Working with sheep, Inglis *et al* (1959) noted that the hypomagnesaemia was associated with a rise in temperature in the spring accompanied by considerable rainfall—conditions for rapid growth of grass

A factor which contributes to the greater incidence of hypomagnesaemia observed when nitrogen and potassium fertilizers are used

together is the considerable pasture contamination with urine, high in potassium, which follows the intensive stocking made possible by the fast growth of grass. Pasture fertilization may also exert an indirect effect by changing the botanical composition of the sward, e.g. phosphate and potassium may increase the clovers which are reduced by the application of nitrogen.

The decrease in the incidence of hypomagnesaemia as spring fades into summer could be due to the interaction of three factors: first, the fall in nitrogen and potassium as the herbage matures; second, an increase in herbage magnesium; and third, a greater intake of dry matter and of magnesium, possibly as a result of a lower water content and increased palatability.

Cow's milk is relatively low in magnesium (approximately 0·6 gm. per gallon). Calves older than six weeks are often unable to satisfy their magnesium requirement on a milk diet alone and their skeletal magnesium is mobilized to offset the dietary deficiency. It is thought that this is not a simple dietary deficiency but one which is to some extent conditioned by the simultaneous calcium ingestion (Allcroft, 1960*b*); the higher the calcium content of the milk, the lower the availability of its already low content of magnesium. In addition, the large intestine ceases to be a site of magnesium absorption in older calves.

DRY-MATTER INTAKE

A mere reduction in the intake of dry matter could readily upset a precarious magnesium equilibrium. Some fertilizer treatments affect pasture palatability and thus magnesium intake (Ender, Dishington and Helgebostad, 1957). The sudden change in diet associated with the release from winter quarters may bring with it digestive upsets which may, in turn, reduce appetite and magnesium intake. On the other hand, scouring may accompany such a dietary change and cause an increased faecal loss of magnesium. Rook and Balch (1958) showed that the intake of magnesium by individual animals varied from 9·5 to 15·2 gm. per day and was largely associated with differences in palatability and dry-matter content of the herbage offered.

THE DEMANDS OF PRODUCTION AND STRESS

If the availability of the dietary magnesium is 25 per cent and the magnesium concentration in cows' milk is 0·6 gm. per gallon, then an additional 2·4 gm. magnesium must be supplied for each gallon of

milk produced It is possible that for high-yielding cows this calculation may not be valid since the availability of dietary magnesium may fall at the higher levels of magnesium intake (Graham, Caesar and Burgen, 1960) Since the body of a calf contains only about 20 gm magnesium the magnesium demands of pregnancy are not very exacting However, in beef cows which are still suckling large calves when more than half-way through pregnancy, the demands of pregnancy may be sufficient to lead to the onset of hypomagnesaemia The magnesium demands of growth by a rapidly growing dairy heifer have been recalculated from Blaxter and MacGill (1956) They vary from 2 8 gm per day at 150 lb live weight to 6 2 gm per day at 1,000 lb live weight, assuming an availability of dietary magnesium of 25 per cent The onset of oestrus often serves as a precipitating factor under conditions when a marginal magnesium balance is to be expected The reason for this is unknown though it may take place as a result of an increase in physical activity and thus an increase in the metabolic demand for magnesium

Cold, inclement weather is also thought to precipitate cases of hypomagnesaemia (Allcroft, 1947*a*) Confirmatory evidence for this was obtained in New Zealand by Christian and Williams (1960) who found that hypomagnesaemia was induced in fasting sheep much more rapidly if, at the same time, they were exposed to cold and wet weather This phenomenon is probably caused by a rise in basal metabolic rate operated through the thyroid gland Such a rise was produced in cows by Swan and Jamieson (1956) by the use of thyroprotein A fall in serum magnesium concentration accompanied this thyroprotein administration

TREATMENT

The utmost urgency is necessary not only because death can intervene very quickly but also because of the considerable bodily harm which the animal may suffer during a series of convulsions Recumbent cases are often treated with a combined solution which contains magnesium, calcium and phosphate. It is best administered intravenously and may be followed by the injection of aqueous magnesium sulphate subcutaneously Drugs such as chlorpromazine are helpful in controlling the muscular spasms Pentobarbitone or chloral hydrate has been used as a sedative in order to minimize the effect of such extraneous disturbances as noise, since these may precipitate convul-

sions. The oral administration of calcined magnesite (magnesium oxide) at the rate of 2 oz. per day should be started immediately and continued for as long as the animal is likely to remain at risk. When it is possible, the affected animal should be housed and given dry food for at least a week after a period of hypomagnesaemia.

PREVENTION

As mentioned earlier, in order to maintain the plasma magnesium concentration at the level of the renal threshold for magnesium the rate of magnesium absorption from the alimentary tract must balance the rate of endogenous faecal magnesium excretion plus any requirement for production. In a wether (male castrated sheep) of constant weight this rate of excretion amounts to about 200 mg. a day. The period of risk might last a month so that the amount of magnesium which must be absorbed over that period is about 6 gm. This could be provided either by increasing the dietary magnesium in some way or by the implantation of a magnesium compound so that the vagaries of absorption from the alimentary tract could be avoided. Attractive though this latter solution would seem to be, it is impractical on account of the large size of the implant required, even if magnesium oxide were used. Moreover, there are serious difficulties associated with the manufacture of implants of such a composition that they dissolve slowly and are not sealed off from the body by a capsule of fibrous tissue (Care and Jones, 1960).

ORAL ADMINISTRATION OF MAGNESIUM COMPOUNDS

The alternative to injection or implantation is some form of oral administration, since it is now well established that daily oral supplements of magnesium compounds can largely prevent the onset of hypomagnesaemia (Ender *et al.*, 1949; Allcroft, 1953; Bartlett *et al.*, 1954). Olivant, Manktelow and Hemingway (1960) have carried out trials on sheep using a rumenal bullet of a magnesium-rich ceramic. The preliminary results appear promising though difficulty has sometimes been encountered during the introduction of such a bullet. In Holland, Seekles and Boogaerdt (1956) have given daily doses of 50 gm. magnesium oxide in palatable fodder cake from about 1 week before cows were turned out to pasture. The incidence of hypomagnesaemia was reduced to about one-quarter of the level in untreated controls provided that the administration was done continuously

throughout the period at risk Work in England (Allcroft, 1954, Line *et al*, 1958) showed that a daily dose of 2 oz magnesium oxide given as a drench to milking cows turned suddenly from winter-stall conditions on to a quickly growing, lush pasture, was an effective method of control They also showed that similar amounts were effective, mixed with a small quantity of crushed oats and fed in troughs to outwintered dry dairy stock Under conditions conducive to hypomagnesaemia, they demonstrated that serum magnesium concentrations fell to dangerously low levels within two days of cessation of oral magnesium supplementation, even though a high intake of magnesium had been given daily for several weeks previously This illustrates the point already made that the adult animal has no means of storing magnesium in a readily available form The daily ingestion of 2 oz. of magnesium oxide did not cause an abnormal increase in serum magnesium levels although Care (1960*a*) showed that 4–8 oz. could produce hypermagnesaemia in fattening bullocks

Line *et al* (1958) considered that if the average loss from hypomagnesaemia was more than 1½ per cent of the cattle at risk it would be profitable to feed magnesium oxide daily in the cubed concentrates to all cows for a month, starting a few days before the commencement of grazing

The level of dietary supplementation with magnesium oxide for sheep is recommended at ¼–½ oz. per head per day mixed with crushed oats and offered in troughs However, some sheep may eat considerably more than their share and may scour in consequence (Allcroft, 1960*a*) Up to 1 oz. magnesium oxide per day has been fed to ewes during pregnancy and lactation with no ill effect other than some scouring (Care, 1960*c*)

Magnesium oxide is considered by many to be unpalatable to stock so that it has often to be fed as a paste with molasses, or as a magnesium-supplemented cattle cake It may also be sprinkled on silage just prior to feeding, or grass at the silo may be treated with magnesium sulphate (McDonald and Jackson, 1955)

It is possible that the odd cases of hypomagnesaemia noted in animals of the same age and breed with access to magnesium supplements may be caused either by some individual idiosyncrasy characterized by a very low capability for absorbing magnesium or by those animals not getting their fair share of the supplement.

Although no adverse effects on condition, milk yield, fertility and serum calcium, magnesium and inorganic phosphate levels have been

noticed by Allcroft (1960*a*) in Ayrshire cows after six months of a daily 2 oz. oral supplement of magnesium oxide per head, higher levels, viz. 6 oz. have been shown to cause scouring and a slight decrease in plasma calcium concentration (Care, 1960*a*). This dose was fed for a few days only so that it is possible that this high level of supplementation might have had deleterious effects if continued for some time.

The amount of supplementary magnesium oxide required by calves depends on the age of the animal and the available dietary magnesium but usually $\frac{1}{4}$–$\frac{1}{2}$ oz. magnesium oxide or $\frac{1}{2}$–1 gm. magnesium carbonate should be given daily. This amount will also serve to restore a normal magnesium status in a hypomagnesaemic calf. Excess oral magnesium therapy may produce rickets in young stock, possibly as a result of the competition of calcium and magnesium for the same absorptive mechanism, as has been shown in rats by Alcock and MacIntyre (1960).

FERTILIZER TREATMENT OF PASTURES WITH MAGNESIUM COMPOUNDS

Because of the difficulties involved in the use of oral magnesium supplements under some conditions, a number of workers have been investigating the efficacy of magnesium fertilizer treatment as a means of increasing the magnesium content of the pasture. In New Zealand Cunningham (1936*a*) showed that the application of 8 cwt. of magnesium sulphate per acre increased the magnesium content of the sward by about 18 per cent. He also employed magnesium limestone in amounts equivalent to 8 cwt. magnesium sulphate per acre but found that the effect was more delayed and less persistent than that obtained with the magnesium sulphate. Bartlett *et al.* (1954) used calcined magnesite (magnesium oxide) at the rate of 25 cwt. per acre to raise the pasture magnesium content by nearly 100 per cent. Moreover, the incidence of hypomagnesaemia was reduced and the effect on the herbage persisted for at least 2–3 years. Parr and Allcroft (1957) compared the effects of $2\frac{1}{2}$ tons of magnesium limestone per acre with that of 10 cwt. of magnesium oxide per acre; they found the latter more effective in raising pasture magnesium concentration and in the prevention of hypomagnesaemia. They suggested that the simultaneous application of calcium in the magnesium limestone antagonizes the uptake of magnesium (Hunter, 1949). Although a level of magnesium oxide application of 10 cwt. per acre is uneconomic if its beneficial effects are only to last one year, this pasture, as treated

by Parr and Allcroft (1957) has given protection against hypomagnesaemia for the six subsequent grazing seasons, whilst hypomagnesaemia occurred on the adjacent plot. The plot top-dressed with magnesium limestone also gave protection against clinical cases of hypomagnesaemia for six years, but each year there was a slight fall in serum magnesium levels during the first few days of grazing, followed by a return to normal levels Trials are at present in progress to investigate the long-lasting protective effects of magnesium oxide applied at about 5 cwt per acre under a wide variety of climates and soil conditions. It is thought that such treatment would be an economic method of control of hypomagnesaemia for some methods of husbandry (Allcroft, 1960*a*)

It is difficult to devise sure methods of prevention of hypomagnesaemia for beef herds on intensive grazing, for ewes with lambs and for suckling beef calves In these cases, the problem may be solved by top-dressing the pastures with powdered magnesium limestone or with magnesium oxide if the lime status of the soil is already high Perhaps the best method to limit hypomagnesaemia in suckling ewes is to allow access to a 'run-back' of unfertilized, permanent pasture since this does not grow so rapidly as a reseeded, top-dressed pasture and is generally accepted to be less associated with hypomagnesaemia.

Finally, the onset of hypomagnesaemia can often be prevented by feeding hay before turning the cattle out to grass each day, this is a more reliable method than setting up hay racks in the field where individual animals may decline to use them

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CHAPTER TWENTY-FIVE

Copper Deficiency and Molybdenum Excess

RUTH ALLCROFT

Introduction—Copper and molybdenum levels in animal tissues and in plants—Copper deficiency in sheep and cattle—Molybdenum toxicity—Aetiology of copper deficiency diagnosis and treatment—Copper poisoning—Conclusion

The essential physiological role of copper was first demonstrated in 1928 when the Wisconsin workers (Hart *et al*) showed that it was necessary for the formation of haemoglobin in the rat During the next decade, its importance for animal health was indicated when investigators in various parts of the world showed that a deficiency of copper was associated with naturally occurring diseases of cattle and sheep The first reports by Neal, Becker and Shealy (1931) suggested that 'salt sick', a wasting disease of cattle in parts of Florida, was related to a copper deficiency, but later work (Neal and Ahman, 1937) showed that it was due to a deficiency of both copper and cobalt Similarly, in 1933 Sjollema reported that *likzucht*, a licking and wasting disease affecting cattle, sheep and goats in some parts of the Netherlands, was due to a copper deficiency in herbage and animals, although it is now generally accepted by Dutch workers (Russell and Duncan, 1956) that *likzucht* is due primarily to a deficiency of cobalt

The work of Bennetts and Chapman in 1937 was of primary importance They found that enzootic ataxia, a demyelinating disease of lambs in Western Australia, was prevented by administration of copper to the ewes during pregnancy and that copper given to the lambs arrested the progress of the delayed' type of the disease which sometimes occurs in lambs from 1 to 6 months of age This was

confirmed in South Australia by Marston *et al.* (1938) and by later reports of the Western Australian workers (Bennetts and Beck, 1942) who related the condition to a copper deficiency in both animals and pasture. About the same time Bennetts and his colleagues reported another enzootic disorder of dairy cattle known locally as 'sudden death' or 'falling disease' which was shown to be caused by a deficiency of copper in the pastures and in the animals.

Since this pioneering work, copper deficiency syndromes in sheep and cattle have been reported from many parts of the world. Later work has indicated, however, that these disorders are not all related to a simple deficiency of copper in the herbage. Depletion of copper stores can occur in stock on pastures containing apparently adequate and even high concentrations of copper and it is evident that factors other than a dietary deficiency of copper are concerned. Under these circumstances the condition is sometimes referred to as an 'induced', 'complicated' or 'conditioned' copper deficiency. Because of these complications it is necessary to discuss the metabolic relations between copper and other dietary constituents which affect storage and utilization of copper in the animal. Of these the most important so far known is molybdenum, since it has been shown that a reciprocal antagonism exists between copper and molybdenum in ruminant nutrition, but much is still unknown concerning copper metabolism in the ruminant; some of the complexities will become evident in subsequent sections.

In this chapter, it is proposed to discuss the occurrence, symptoms and aetiology of copper deficiency in sheep and cattle in Britain and to relate them to similar conditions in other countries. Before doing this it may be helpful to give some indication of the physiological role of copper and molybdenum and the concentrations found in animal tissues and herbage.

COPPER LEVELS IN ANIMAL TISSUES AND PLANTS

Its universal occurrence in biological material indicates the essential nature of copper in the nutrition of plants and animals even though its precise function is not yet known. It is assumed that like other trace elements, it acts as a catalyst in some enzyme systems. Recently Wainio, Wende and Shrimp (1958) confirmed the original suggestion of Keilin and Hartree (1938) that cytochrome oxidase contains copper,

and Anderson and Tove (1958) have reported that copper has a direct function in the synthesis of haem Because of its presence in most of the tissues copper probably takes part in a diverse number of functions in the body, thus accounting for the range of clinical and pathological manifestations of copper deficiency observed in the same or different species

Copper has been found in all tissues of the body in varying concentrations but is present in greatest amounts in the liver, which is the main storage organ of the body and therefore liver values give a reasonably reliable index of the copper status of the animal

Beck (1956) has determined liver copper concentrations for a wide range of animal species including mammals, birds, fish, reptiles and amphibia and has found that normal adults for most species have liver copper concentrations of 10–50 p p m dry matter (D M) A few species have liver values outside this range and notable exceptions are sheep and cattle whose normal range is much higher Values (expressed as p p m dry matter) for normal sheep and cattle in New Zealand have been given by Cunningham (1946) adult cattle range from 23 to 409 with a mean of 200, adult sheep from 171 to 1,374 with a mean of about 500 for two-tooth wethers and 600 for aged ewes Data obtained at the Central Veterinary Laboratory, Weybridge, from many samples from different parts of the country over about 10 years show a similar range for cattle, but the range found for sheep is lower—about 30–800 with a mean in the region of 200 p p m. D M In most species, the newborn have a higher liver copper concentration than normal adults but during the suckling period the concentration falls (Underwood, 1956) Sheep are a notable exception to this Cunningham (1946) reported that both concentration of copper and total copper content of the liver of sheep increased with age In cattle he found a decrease in copper concentration from newborn calf to yearling stage and a subsequent rise in adult livers

It is generally accepted that when liver copper concentrations fall below about 20 p p m in cattle of any age, deficiency symptoms are likely to occur Ewes with values below about 15 p p m during the last two months of pregnancy may have ataxic lambs, liver copper concentrations of ataxic lambs are usually below 10 p p m. When excessive amounts of copper are ingested, the liver can accumulate large amounts without harmful effects until a certain level is reached. Above this, which in sheep and cattle is about 1,000 p p m. and upwards, copper may suddenly be liberated into the blood stream

causing haemolysis, jaundice and usually death. This effect will be discussed in more detail in the section on copper toxicity.

It is customary to use whole blood samples for estimation of copper since the distribution is about equal between cells and plasma in sheep and cattle (Eden and Green, 1939; Adams and Haag, 1957). Although blood copper levels are not such a reliable index as liver copper concentrations they provide a satisfactory indication and are adequate for field work provided samples are taken from a representative number of animals from the group under investigation. A single sample from an individual animal may be of little diagnostic value, especially in the case of sheep where the variation in individual members of a flock may be very wide—as much as tenfold—even when there is no history of ataxia in the lambs (Eden, 1941).

The generally accepted normal range for blood copper values for sheep and cattle is about 70–170 µg./100 ml. (0·07–0·17 mg./100 ml.) but only a small proportion exceed 120 µg. and a common average value is 100 µg./100 ml. (0·1 mg./100 ml.). When the majority of values for a flock or herd are below 70 µg./100 ml. it is usually an indication of a low copper status and clinical symptoms are likely to occur.

In an investigation of blood copper levels in a wide range of vertebrate species, Beck (1956) found that among placental mammals, highest levels occurred in the pig (140 µg./100 ml.), relatively low levels in the guinea-pig and rabbit (30–60 µg./100 ml.) and the rat, sheep, cow and man showed intermediate levels (*c.* 100 µg./100 ml.). The lowest values occurred in the domestic fowl and turkey (20–30 µg./100 ml.).

Since copper deficiency symptoms can occur in stock on pastures containing high as well as low concentrations of copper, it is not possible to postulate a herbage content which will ensure a normal copper status in cattle or sheep eating it. It is generally accepted, however, that the copper content of 'normal' pastures ranges from about 7 to 30 p.p.m. D.M. with common 'normal' values lying within the range of 8–20 p.p.m. and that deficiency disorders are likely to occur when the concentration is less than 5 p.p.m. Beck (1951) reported that severe copper deficiency symptoms are found in stock in Western Australia on pastures containing less than 3 p.p.m. D.M., that pastures containing 3–6 p.p.m. are marginal and that stock remain healthy on those with a copper content about 6 p.p.m. The copper content of various botanical species differs and the concentration present in mixed herbage at any given time will depend on a number of factors such as

the botanical composition, stage of growth, the cutting and grazing management and on the 'available' amounts of copper in the soil It is therefore necessary to take samples at intervals throughout the year before an assessment can be made of the amount of copper any particular pasture may supply to the grazing animal The presence in some herbage of compounds which inhibit the storage of copper in ruminants means that its copper content may be of limited value in assessing the amount available to the animal and that in Britain at least, it is not possible to predict the probable copper status of cattle and sheep by estimation of the copper content of the pastures they are grazing

A study of the chemical forms in which copper is present in herbage and their availability to animals was studied by Mills He showed (1955) that grass contains a stable water-soluble copper complex which has a greater effect than inorganic copper in restoring the haemoglobin and hair pigmentation of rats maintained on a copper-deficient diet His more recent work (1958) suggests the possibility that copper is absorbed directly in the form of an as yet unidentified complex or complexes

MOLYBDENUM LEVELS IN ANIMAL TISSUES AND PLANTS

During the last 25 years molybdenum has been shown to be one of the trace elements of agricultural importance For some time it has been known to be essential for the growth of the nitrogen-fixing soil organism *Azotobacter* and for nitrogen fixation by the legume symbiote *Rhizobium* sp The presence of minute amounts in a wide variety of plant and animal tissues was reported by Ter Meulen (1932) and in 1946 Anderson demonstrated a marked response of some pasture plants in Australia to very small applications of molybdenum Marked improvement in pasture and crop yields from the use of molybdate fertilizers has been reported in certain areas in New Zealand (Davies 1952) but since too much molybdenum can produce harmful effects in stock the concentration of molybdenum in pastures is important

It is generally accepted that a pasture molybdenum content of 1–3 p p m D M is normal and on present evidence is not likely to cause disease in animals However Cunningham (1960) has shown that the harmful effects of molybdenum on cattle are related to the amount of copper as well as molybdenum present in the food if the copper content is low a moderate excess of molybdenum may be harmful,

but with a normal copper content, greater amounts of molybdenum must be present before toxic effects are produced. It has also been shown by Dick (1953) in Australia that molybdenum will not reduce liver copper storage in sheep unless sufficient inorganic sulphate is also present in the diet. These observations and the fact that molybdenum is an integral component of the enzyme xanthine oxidase (de Renzo *et al.*, 1953) indicate that it plays an essential role in animal metabolic processes. Underwood (1956) repotts that vertebrate tissues are normally very low in molybdenum, mammalian muscle tissue usually containing 0·05–0·10 p.p.m. D.M. with similar or slightly higher concentrations in otber tissues except the liver where values between 1 and 3 p.p.m. are common. Variable concentrations for liver, spleen and kidney cortex have been found for 'normal' cattle and sheep in Great Britain varying from 1 to 10 p.p.m. but most commonly of the order of 2–4 p.p.m. Even when high intakes of molybdenum were given for long periods (800 mg. daily to cattle for a period of 18 months and 200–280 mg. daily to sheep for about 7 months), liver molybdenum values did not exceed about 140 p.p.m. and rapidly fell to normal levels when molybdenum supplementation was stopped.

Tissue molybdenum levels in sheep are not dependent only on molybdenum intakes. Dick (1956) has shown that tissue retention is influenced by the amount of inorganic sulphate in the diet. When this is high, molybdenum excretion is increased and tissue retention decreased.

COPPER DEFICIENCY IN SHEEP

A nervous disorder of new-born and young lambs characterized by inco-ordination of gait has been reported (Russell and Duncan, 1956) from many parts of the world. It is known under a variety of local names such as *swayback*, *swingback*, *warfa*, *Gingin rickets*, *enzootic ataxia*, *lamkruis* and *renguerra*.

GREAT BRITAIN

In Great Britain it was first described in 1932 by Stewart and subsequent investigations by Innes and Shearer (1940) showed that its geographical distribution is widespread throughout England, Wales and parts of Scotland. The incidence, however, is erratic and may vary considerably from year to year in the same districts and on the same farms. Before prophylactic measures were introduced, the

mortality in severely affected areas varied annually from 1 to 50 per cent of the lambs. Ewes of any breed or age may give birth to ataxic lambs but occurrence and incidence are broadly related to length of sojourn on affected farms, although ewes may produce healthy and affected lambs in successive years.

The symptoms and pathology have been comprehensively described by Innes and Shearer (1940) and may be summarized as follows. In some cases lambs are severely affected at birth and in others symptoms are delayed and may develop as late as three months after birth—the longer the period before onset of symptoms the milder is the disease. The symptoms are those of ataxia and vary in degree of severity. All cases show inco-ordination of movements, severe cases are sometimes blind and are unable to stand or walk, others may rise and walk with difficulty, whereas mild cases show only slight weakness of the hind quarters, particularly when made to move quickly.

Severely affected lambs usually die shortly after birth but mild cases, usually of the delayed type which show only slight non-progressive inco-ordination, often survive, and when bred from later, may produce normal lambs. Mothers of affected lambs remain apparently healthy and show no clinical symptoms.

The characteristic pathological pattern is still a matter of controversy. Innes and Shearer (1940) described it as a diffuse symmetrical demyelination of the cerebrum, varying in extent from small foci in the *centrum ovale* to gross demyelination of the whole hemisphere with liquefaction and cavitation in extreme cases. Secondary degeneration of the motor tracts in the cord is always present in affected lambs. Evidence indicates that demyelination occurs at a relatively late stage of gestation, perhaps within the last six weeks, i.e. after cerebral myelination has begun. Romanes (1947) has shown that the first myelin appears in the forebrain of the lamb at 96 days. Amyelination rather than demyelination has been suggested but evidence for this is still incomplete.

Liver and blood copper values of affected lambs and their mothers are low and the greatest incidence of the disease occurs in lambs from ewes with blood copper values between 10 and 60 µg/100 ml. But low blood copper levels do not indicate that swayback will inevitably occur. It has been shown (Eden, 1941) that there is frequently a wide variation in blood copper levels in individual members of flocks on farms with no history of swayback and this variation can be as wide as tenfold, so that blood copper values of 10–100 µg/100 ml may be

found in healthy flocks. An individual blood copper value, is, therefore, of no diagnostic significance, but if the blood copper status of a flock of ewes is low during pregnancy, it is possible that swayback may occur. Although low blood and liver copper values have always been found in affected lambs and their mothers, equally low values have been found unassociated with demyelination or of clinical manifestations of swayback. At present both field and experimental evidence indicates that a low copper status alone does not necessarily produce the lesions of swayback: it seems that demyelination is the result of other metabolic defects which operate only when the copper status of both ewe and lamb is low.

Gallagher, Judah and Rees (*1956a, b*) showed that in uncomplicated copper deficiency in rats, the major metabolic disturbances were loss of cytochrome oxidase activity and the suppression of phospholipid synthesis. They found that haem α was almost completely absent from copper-deficient tissues and suggested that this was the limiting component of the cytochrome oxidase system. Recently Howell and Davison (1959) reported a significant reduction in copper content and cytochrome oxidase activity in the brain of swayback lambs compared with normal lambs.

Anaemia is not common either in affected lambs or their mothers and no other abnormality of the blood picture has been observed in ewes with a low copper status or in swayback lambs. Unthriftiness is not specifically associated with copper deficiency in sheep and the abnormalities of the fleece which Australian workers (Bennetts and Beck, 1942; Lee and Moule, 1947; Marston, 1951) have shown to be the first symptom of copper deficiency in Merino sheep have not been reported in Britain.

AUSTRALIA

The disease in Australia is more prevalent among lambs of 3–8 weeks of age than among new-born lambs and, although the brain lesions may not be as extensive as those reported in swayback lambs in Britain by Innes and Shearer (1940), Australian and English investigators are satisfied that the two diseases are pathologically similar.

Apart from important aetiological differences, there are differences in symptoms attributed to copper deficiency in sheep in Australia, New Zealand and Britain. Bennetts and Beck (1942) reported that 'stringiness' of wool, loss of condition and diarrhoea occurred in ewes in Western Australia during late pregnancy and lactation, and that a

severe concurrent anaemia in ewes near to parturition could be correlated with an acute form of ataxia in the lambs. Adequate copper supplementation prevented these symptoms and promoted optimal growth in lambs. Non-breeding sheep were able to maintain normal health even when blood copper levels were very low, anaemia was only rarely found and 'stringiness' of the wool was the only clinical sign of copper deficiency observed.

In the 'coast disease' area of southern Australia, Marston, Lee and McDonald (1948) studied the pattern of symptoms which developed in progressive, uncomplicated copper deficiency in sheep kept on a cobalt- and copper-deficient area by providing a cobalt supplement. They reported that the first sign of copper deficiency is defective keratinization of the wool, as the copper status is further reduced, a hypochromic anaemia and loss of weight occur, when the copper reserves of the ewe are very severely depleted, demyelination in the central nervous system of the lamb occurs.

The effects of copper deficiency on pigmentation and keratinization of the hair have been fully described by Marston (1950, 1952). He and his colleagues have shown that abnormalities of the fleece of Merino and Merino cross-bred sheep, referred to as 'stringy' or 'steely' wool are a specific and early indication of copper deficiency. Depending on the degree of depletion, progressive loss of crimp occurs until in severely deficient animals, straight lustrous fibres entirely devoid of crimp are produced. In some areas, a weakness of the fibre has also been reported (Lee and Moule, 1947). As soon as the copper status of the sheep is restored to normal a spectacular reappearance of the crimp and of the colour in black sheep occurs. Lee (1956) has shown that this characteristic wool lesion is not confined to Merino sheep but also occurs in copper-deficient Border Leicester, Romney Marsh, Lincoln and Dorset Horn ewes in South Australia. It is of interest that this specific lesion has not been observed in British breeds in other countries where copper deficiency in ewes has been confirmed, (Cunningham, 1950, Green, 1951, Stewart, 1951). Some loss of pigmentation has, however, been noted by Heath (1954) and by Allcroft and Lewis (1956*b*) in copper-deficient Swaledale ewes in which the fleece becomes harsh and bleached, although no other physiological symptoms of copper deficiency were observed in the ewes or in their lambs. This apparent absence of the specific wool lesion in copper-deficient sheep in Britain may be due to lack of careful observation and to the fact that most studies of copper deficiency in sheep in Britain have been made on

small mountain breeds which have long, straight, hair-like wool with little natural crimp.

NEW ZEALAND

Copper deficiency in sheep and lambs in New Zealand has been investigated and reported by Cunningham (1946 and 1950). The disease resembles that observed in Great Britain in so far as there are no wool lesions in breeds originating from Britain, anaemia and unthriftiness do not occur in adult sheep, and there is no retardation of growth in lambs not affected by ataxia. It differs in that (1) an acute osteoporosis predisposing to fractures may occur in lambs as a result of a copper deficiency less pronounced than is necessary to cause ataxia; (2) symptoms of ataxia occur only in lambs between the ages of 3 weeks and 4 months, but they are similar to those described for milder cases of enzootic ataxia in Australia and swayback in Great Britain; acute cases associated with brain cavitation have not been observed. The occurrence of osteoporosis associated with copper deficiency in sheep has not been reported from other countries.

6 p p m D M (mean 2 1) compared with 37–231 p p m (mean 122) for healthy cows from sound areas

Copper deficiency in cattle has since been reported from many parts of the world associated with a variety of clinical symptoms, but only in Florida has sudden death similar to that occurring in falling disease been reported (Davis, *1950*)

In 1944 Cunningham reported a disease affecting dairy cows on reclaimed swamps and peaty soils in New Zealand The condition, known locally as 'peat scours' is characterized by severe debilitating diarrhoea during a flush growth of pasture, unthriftiness and marked reduction in milk and butterfat production Young stock are affected even more than adults, and yearlings may die if left on affected land Marked bone fragility occurs in calves from about the age of three months in some areas Similar symptoms occur in beef cattle, but loss of body condition during scouring is not as marked as in dairy cows

Evidence establishing copper deficiency as the cause of the disease was reported (1946) less than normal amounts of copper were found in the herbage and in blood and liver in stock raised on affected land, the condition could be prevented by administration of copper to the animals or by top-dressing the pastures with copper Cunningham (1946) considered that a simple copper deficiency could not explain all the symptoms of the disease and suggested that it may be the result of a small excess of molybdenum in the herbage superimposed on a moderate deficiency of copper Later work by Cunningham (1950) confirmed this view and demonstrated that an increased intake of molybdenum reduced liver copper storage in cattle, reduced growth rate in calves and produced a clinical picture of scouring and un-

of grasses and clovers were found, but in other areas where similar symptoms occurred in cattle, normal pasture molybdenum values were reported (Russell and Duncan, 1956).

Disorders in cattle related to copper deficiency have been reported from Florida (Davis, 1950) and from Ireland (Walsh *et al.*, 1951–2). On pastures in the Everglades in Florida containing 2–4 p.p.m. Cu, emaciation, depigmentation and bone abnormalities have been observed in calves and young cattle and falling disease sometimes occurred in older cattle. Recovery occurred after treatment with copper and the disorder could be prevented by use of copper fertilizers. Kretschmer and Beardsley (1956) considered that the evidence so far obtained gave no clear indication whether molybdenum did or did not affect the copper status of animals in the Everglades.

In Ireland the clinical condition is similar to that occurring in Britain, pasture copper values are within the normal range but molybdenum levels are usually high, ranging from 5 to 20 p.p.m. It is considered that the copper deficiency is induced by the high molybdenum content of the pastures (Neenan, Walsh, and O'Moore, 1956).

It was not until 1946 that copper deficiency was suspected and confirmed (Jamieson and Russell, 1946; Allcroft, 1946) in cattle in Great Britain although it had been known for eight years that swayback was associated with a low copper status of ewes and lambs. Since then, copper deficiency in cattle of all breeds and ages from about three months upwards has been found in many different parts of the country. It is usually found in varying degrees of severity in cattle on 'teart' (Lower Lias clay) and peaty areas but is by no means limited to these soil types. As stated previously, the condition generally occurs on pastures of normal copper content within the range of 7–25 p.p.m. D.M. but values below 5 p.p.m. have been observed. Barlow *et al.* (1960) found that about 62 per cent of 37 samples of 'swayback' herbage taken between May and August in Scotland, had a copper content of less than 5 p.p.m. D.M. Field (1957) reported the copper content of monthly herbage samples throughout a twelve-month period from fields on which copper deficiency in cattle occurred; lowest levels (4·4–7·5 p.p.m.) were found in May and June when the grass was growing rapidly but mean values for the year ranged from 9·3 to 17·2 p.p.m. D.M.

SYMPTOMS

A variety of clinical manifestations have been ascribed to copper deficiency in the bovine, but none are specific and there are no character-

istic lesions nothing resembling the neonatal demyelination of lambs has been reported in calves in Britain The chief effects are progressive loss of condition in adult cattle and unthriftiness and retardation of growth in calves and young stock, the coat becomes rough, dull, discoloured and frequently there is greying or loss of hair, especially around the eyes Diarrhoea is sometimes but not always present and concurrent anaemia is uncommon In beef herds the first symptoms may appear in calves at about three months of age, they often show a stilted gait, particularly of the hind limbs and in extreme cases there is pronounced emaciation and death may occur In some seasons the condition develops more rapidly and severely than in others (Jamieson and Allcroft, 1950) Affected calves often improve when housed or yarded during the winter, but development usually remains subnormal In dairy herds, loss of production in milking cows has been observed (Allcroft and Parker, 1949) but often the most severe symptoms are shown by yearling to first-calving animals Reports have been made associating infertility with copper deficiency in cattle, particularly in heifers, but further evidence on this aspect is required

Under some conditions cattle can have a low copper status without showing any clinical abnormality In beef herds, calves may show severe clinical symptoms while their mothers show none It would appear that the copper requirements are greater for the young growing animal than for the adult and that stress due to poor husbandry may also increase requirements

in old grass. It was demonstrated that the condition could be reproduced in stalled animals by dosing with sodium molybdenum or by putting cattle on to any rapidly growing pasture dressed with a sufficient amount of molybdate to bring the molybdenum content up to 'teart' levels.

The disease occurs during the spring and autumn flush of grass. Milking cows and young stock are chiefly affected and severe persistent diarrhoea may commence within a few days of grazing affected pastures. Milk yield is depressed, the animals develop harsh, staring, discoloured coats, lose condition rapidly and will suffer permanent injury oe death if left on the pasture too long. No inflammation or local damage in the alimentary tract of severely scouring 'teart' animals has been found (Muir, 1941). Recovery is rapid after transfer to non-teart pastures.

Because of the similarity to a scouring disease in cattle on the Wieringermeerpolder in Holland where administration of copper was found to be curative and preventive (Brouwer, 1938), Ferguson *et al.* (1943) tried the effect of copper, cobalt and iron salts. Copper sulphate was found to be effective and extensive field trials showed that drenching or feeding cows with 2 gm. copper sulphate and young stock with 1 gm. per head daily cured and prevented the disorder and maintained animals in good health throughout the 'teart' season.

In a review of the literature Russell (1944) suggested that an abnormal intake of molybdenum might interfere with the utilization of copper and that therefore 'teart' might be a 'conditioned copper deficiency'. Later Dick and Bull (1945) reported that a high molybdenum intake reduced the storage of copper in the livers of cattle and sheep. Soon afterwards the association of molybdenum with 'peat scours' in cattle in New Zealand and its limiting effect on liver copper storage was demonstrated by Cunningham (1946 and 1950). Ferguson *et al.* did not investigate the copper status of animals in the 'teart' area, but a series of investigations started at the Central Veterinary Laboratory, Weybridge, in 1947 showed that cattle which had not had prophylactic copper supplements had low blood copper values of the order of 20–60 µg./100 ml.; heifers of normal copper status sent to a 'teart' farm commenced scouring in one to two weeks and blood copper fell from normal to low levels after two to three months. The scouring effect of high intakes of sodium molybdate to stalled and grazing animals was confirmed. Administration of smaller amounts, insufficient to cause diarrhoea, showed that liver copper storage was significantly

reduced when given over a long period Later Allcroft and Lewis (1956*b*) showed that scouring and loss of condition could be produced in stalled animals by continued intravenous or oral administration of molybdenum before liver copper values had fallen to deficient levels It appears, therefore, that scouring and loss of condition in cattle can occur as a result of molybdenosis without a concomitant hypocuprosis If, however, a high intake of molybdenum is continued over several months, liver copper storage will be reduced ultimately to deficiency levels when the scouring effect of molybdenum becomes more persistent and severe Scouring disorders similar to that on teart pasture have been reported in California and Nevada (Britton and Goss, 1946, Barshad, 1948, Dye and O'Harra, 1959), in Manitoba (Cunningham *et al*, 1953) and in Ireland (O'Donovan, 1949) It should also be mentioned that aerial contamination of pastures by gaseous effluents containing molybdenum from certain industrial works, can produce symptoms similar to those found on natural teart pastures (Buxton and Allcroft, 1955, Parker and Rose, 1955) Herbage molybdenum values as high as 126 p p m D M were found associated with diarrhoea, severe loss of condition and low blood copper levels in cattle Copper supplementation cured the disorder and prevented further occurrence

THE AETIOLOGY OF COPPER DEFICIENCY

The chief difference between copper-deficiency syndromes in sheep and cattle in Australia and in Great Britain, is that in the former region they are associated with pasture copper values which are regarded as deficient, whilst in the latter they occur on pastures containing apparently adequate or even high concentrations Under Western Australian conditions Beck (1941) regarded pasture values of over 5 p p m as supplying adequate copper for health although he pointed out that in some seasons other 'factors' appeared to influence the availability of copper in the plant to animals Marston (1952) considers that enzootic ataxia in Australia is a manifestation of extreme copper deficiency in the sheep arising from a dietary deficiency of copper

In Britain, the occurrence of swayback has not been related to a low copper content of the pastures, values ranging from 7 to 20 p p m D M or more have been found for pastures on which the disease has occurred (Allcroft, 1952) This suggests that other factors are concerned which interfere with the metabolism of copper in the animal A high lead content of herbage was suggested as a contributory factor, but this was

not substantiated. An increased incidence of the disease has been associated with heavy liming of pastures but no real evidence for this has yet been recorded. Workers in Australia and New Zealand (Dick and Bull, 1945; Cunningham, 1946, 1950; Dick, 1956) have shown that a high molybdenum intake can limit liver copper storage in sheep and cattle, but so far the evidence suggests no relationship between a high molybdenum content of pastures and incidence of swayback in Britain (Stewart, Farmer and Mitchell, 1946; Allcroft, 1952). Allcroft (1952) also showed that administration of relatively large doses of molybdenum over a period of 15 months to stalled barren ewes did not prevent storage of considerable amounts of copper. However, Cunningham (1950) demonstrated a high molybdenum intake could reduce the liver copper of grazing ewes on a normal copper intake and reduce still more the copper transmitted to the foetal lamb, but he was unable to produce ataxia in lambs from ewes fed extra molybdenum for four years. Recently Mills and Fell (1960) have produced marked ataxia with degenerative changes and demyelination in the nervous tissue in lambs from ewes on grass cubes supplemented with sodium sulphate and ammonium molybdate to supply 10 gm. SO_4 and 50 mg. Mo daily throughout pregnancy and the suckling period. The liver copper status of lambs and ewes was low; ataxia was associated with values of less than 5 p.p.m. copper in the lamb liver.

About this time the important work of Dick (1953*a* and *b*) in Australia demonstrated the significance of the inorganic sulphate content of the diet on the inhibiting effect of molybdenum on liver copper storage in stalled sheep. He showed that on a diet supplying an essentially normal intake of copper in the range 3–10 mg. per day and a low normal intake of molybdenum of about 0·5 mg. per day, when the sulphate intake is low (less than 0·5 gm. per day) an increase in the molybdenum intake from 1 to 100 mg. per day will have no effect on either blood or liver copper. But when the sulphate content of the diet is adequate and provides an intake of about 2 gm. per day or more, then as little as 0·5 mg. molybdenum per day will significantly limit copper storage. This led him to suggest that some of the discrepancies in the report of workers in Australia and Great Britain might be due to the different intakes of inorganic sulphate by the animals under the conditions recorded.

Investigations to check this suggestion were carried out on sheep and cattle by Allcroft and Lewis (1956*a*, *b*, 1957). No suitable diets could be found which would supply less than 0·5 gm. sulphate per day and

by Dick's criteria all the feeding stuffs used contained ample sulphate to allow the molybdenum present to exert its full limiting effect. Under these conditions it was found that increasing the inorganic sulphate 3–5 times had no significant effect on liver copper levels in pregnant ewes of low or normal copper status. When the molybdenum intake was increased in varying amounts from 4 to 200 times the basal intake for periods of 5–15 months on diets of constant and ample sulphate content, the results indicated that the limiting effect of molybdenum was influenced by factors such as the copper content of the diet, the initial copper status of the ewes and by foetal requirements. Observations on pregnant cattle showed that addition of molybdenum to the maternal diet caused a highly significant reduction in foetal liver storage, but addition of sulphate either alone or with molybdenum did not produce a significant effect. Other experiments on non-pregnant cattle maintained on constant and adequate copper and sulphate intakes showed that high intakes of molybdenum over a period of 1–18 months caused significant reductions in liver copper concentrations.

The different results produced by variations in animals and diets support Dick's suggestion that previous discrepancies between Weybridge and Australian reports could be accounted for by differences in the conditions under which the trials were carried out.

Allcroft and Lewis (1957) found no significant difference in either copper or sulphate contents of pasture samples from farms in several areas where deficiency symptoms in cattle and sheep had and had not occurred. In all cases, copper concentrations were within the 'normal' range and the inorganic sulphate values showed that ample amounts were present to allow the molybdenum to exert its full limiting effect. This indicated that a difference in sulphate content was not a factor contributing to the occurrence or absence of copper deficiency in animals grazing these pastures. But an excess of molybdenum was found in pastures in some areas where copper-deficiency disorders in cattle occurred, and was regarded as at least a contributing factor in causation of the condition. However, since no significant difference was found in the molybdenum content of pastures on farms where swayback was not known to occur, and on those where it was enzootic, it was concluded that an excessive molybdenum content of the herbage could not be regarded as one of the chief factors causing swayback under naturally occurring conditions.

Cunningham's report (1960) on 'peat scours' in New Zealand indicated that the pathological effect of molybdenum on cattle is determined

by the relative amounts of copper and molybdenum in the pastures. Thus, a moderate excess of molybdenum causes the disorder only if the pasture copper is below normal. For example, if the pastures contain about 10 p.p.m. copper, about 20 p.p.m. molybdenum must be present before toxic effects are produced; for lower levels of copper, the minimum harmful level of molybdenum is lower, so that when pasture copper is 3–5 p.p.m., molybdenum is harmful at levels of 3–7 p.p.m. The relative amounts of copper and molybdenum in pastures from teart and many peat areas are in line with these findings but many pastures from other areas where severe copper deficiency in cattle has occurred have shown relatively high copper and low molybdenum values. In others, molybdenum was either within the normal range or a little above in samples from both healthy and affected areas so that the disorder in these cases could not be attributed to an excess of molybdenum. It seems therefore that the copper: molybdenum relationship reported as harmful by Cunningham (1960) does not hold for all areas of Britain. Indeed, the experimental and filed evidence so far obtained at Weybridge indicates that the copper, molybdenum and inorganic sulphate contents of the food are not the only factors concerned in the occurrence of copper deficiency in cattle and sheep in Britain.

It is evident too, that the copper content of foodstuffs may be of little value in estimating a 'normal' intake of copper for the animal. Underwood (1956) has pointed out that a 'true' or basic minimum copper requirement can be described as one in which all the dietary conditions affecting copper are at an optimum and that such an optimum cannot yet be given. Dick has suggested that crossbred stalled sheep can, under appropriate dietary conditions, be in copper balance on an intake of about 1 mg. per day or less, which is very much lower than had generally been believed possible. His data also indicated that the amount of copper required to replace normal wastage was less than 3 mg. per day and he suggests that where more than this is required by sheep to maintain their copper status, other factors are operating which either impose a limitation on copper assimilation and retention or increase the animal's requirements for copper.

THE DIAGNOSIS AND TREATMENT OF COPPER DEFICIENCY

From the above information it is apparent that it would be difficult to predict the probable copper status of animals from chemical examination of samples of feeding stuffs or soils in Britain.

A suspected deficiency should be confirmed by differential diagnosis and by chemical analysis of blood or liver to assess the copper status This is necessary because copper deficiency causes no clinical abnormality in adult sheep and no specific clinical or pathological effects in cattle In lambs, both pathological and chemical examinations should be carried out to establish a diagnosis for swayback as other conditions may produce similar symptoms Low liver copper values are always found in affected lambs but this finding alone is not proof of swayback, liver copper values within the range found in swayback cases have been found in lambs showing no clinical or pathological signs of swayback.

In both cattle and sheep it is necessary to take blood samples from a representative number of animals in the herd or flock since wide variation in blood copper levels is frequently found among individual members This is especially so in the case of sheep for which individual blood copper values are of little diagnostic value There is no definite correlation between low blood copper values in ewes and occurrence of swayback in their lambs If the copper status of a flock is low, all that can be said is that swayback *may* occur—there is no certainty that it *will* occur

Although the variation in blood copper levels among members of a herd of cattle is usually not as great as among members of a flock of sheep it is preferable to take representative blood samples from various age groups especially from yearling to first calving stage for assessment of the copper status Copper deficiency is a herd problem and therefore individual cases of unthriftiness are unlikely to be associated with it. Since the liver is the main storage depot for copper liver copper figures give the most reliable index of the copper status of an animal and whenever possible they should be used for diagnostic purposes

In spite of the fact that a low copper status of the ewe does not lead inevitably to swayback in the lamb there is ample proof that administration of copper to deficient ewes during pregnancy prevents the disease in lambs

intervals throughout pregnancy or two doses of 1·5 gm., one dose at about eight weeks and the second approximately four weeks before lambing, are effective in preventing the disease. The provision of mineral mixtures or salt licks containing copper are also effective provided all the ewes take enough to supply a protective but not harmful amount of copper. It is sometimes difficult to ensure this and in some instances copperized mineral mixtures have not given adequate protection, and in others have caused toxic effects because of excessive intakes by some individuals.

Allcroft, Clegg and Uvarov (1959) showed that a subcutaneous injection of 45 mg. copper as copper glycine into ewes about mid-pregnancy was an effective method for prevention of swayback and more recently they demonstrated that 50 mg. of copper as a copper calcium ethylenediamine tetra-acetic acid complex is a more satisfactory preparation for this purpose (unpublished data). Prophylactic treatment with copper is necessary only during the gestation period and since no adverse effects have been attributed to copper deficiency in adult sheep in Britain, there would seem to be no reason to continue treatment beyond this period. It should be recognized that sheep are much more susceptible to cumulative copper poisoning than cattle, and can, under some circumstances store dangerous amounts of copper in their livers which may eventually cause toxic effects. For this reason the top-dressing of pastures with copper compounds is not a suitable method of control in Britain.

In cattle, the margin of safety between prophylactic or therapeutic levels of copper and those likely to cause toxic effects, is greater. Even so, caution should be observed in giving copper supplements; if copper deficiency is suspected veterinary advice should be sought.

The effect of treatment of copper-deficient cattle of various ages and types has been observed under controlled conditions in this country and dramatic responses have been recorded (Allcroft and Parker, 1949; Jamieson and Allcroft, 1950; Field, 1957). Various methods of administration have been tried on different farms to get information on optimum dosage levels of copper and to find the most convenient and economical means of supplying adequate amounts under existing methods of husbandry. Copper has effectively been given by mouth as a drench, in mineral mixtures, incorporated in dairy cakes, as a solution sprinkled on the concentrates and administered parenterally by intravenous, intramuscular or subcutaneous routes.

Top-dressing pastures with 5–10 lb of copper sulphate per acre has not been found a satisfactory method of control in Britain where the deficiency is nearly always 'conditioned' or 'induced' In such pastures in which the copper content is already normal or even high, it has been found (Morgan and Clegg, 1958 Jamieson and Allcroft, 1951) that an increase in copper does not always occur even after an application of as much as 10 lb per acre Other objections to this method of control are the need for annual application, the cost of labour, and in particular the risk of copper poisoning in stock grazing pastures contaminated with extraneous copper sulphate

Dosage rates of oral or parenteral copper compounds must depend on the degree of copper deficiency in the animal the route by which it is administered and the severity of the 'conditioning' factors in the foodstuffs which influence the absorption and retention of copper by the animal The method of administration used must also depend on the management and the type of herd involved—methods suitable for milking cows will probably not be suitable for beef animals at grass For example, 2 gm copper sulphate given by mouth daily was necessary to control diarrhoea in dairy cows on strongly 'teart' pastures in Somerset (Ferguson, Lewis and Watson, 1943), 300 mg Cu as a solution of copper sulphate in normal saline given intravenously for experimental purposes was found equally effective for a period of six weeks under similar conditions (Allcroft, 1952) In general it is convenient to give copper supplements by mouth to stalled or dairy cattle which can receive measured amounts at the required intervals For young stock at grass and store animals that are not handled frequently and do not receive concentrate rations, the most satisfactory method of control is by subcutaneous injection of suitable copper preparations In New Zealand (Cunningham, 1957*a*, *b*), in Nevada and California in the United States (Dye and O Harra, 1959) and in Britain (Allcroft and Uvarov, 1959), it has been demonstrated that injection of 120 mg copper as a copper glycine preparation repeated two or three times during he year depending on local conditions, is a safe and convenient method f copper supplementation for beef cattle Recent investigations have ndicated that a suspension of copper calcium ethylenediamine tetracetic acid complex produces greater absorption of copper into the liver nd less local reaction than copper glycine (Allcroft and Uvarov, unpublished data) Again however, it should be remembered that too much copper can have harmful effects

COPPER POISONING

In recent years the use of copper compounds for agricultural and veterinary purposes has considerably increased. They are now widely used in this country in mineral supplements and as additives to feeding stuffs for farm stock as well as for prophylactic and therapeutic treatment. This has increased the risk of copper poisoning and indeed, reports indicate that chronic or cumulative copper poisoning has become more prevalent over the last few years. ('Cumulative' is a more accurate term to apply to this condition since the clinical effect of excessive accumulation of copper is terminally sudden, acute and usually fatal.) For this reason a discussion of the subject has been included.

The continuous ingestion of small amounts of copper in excess of the quantity required for physiological equilibrium leads to accumulation of abnormal amounts in the tissues, especially in the liver which is the main storage depot. There is no unfavourable effect on the animal until certain high levels are reached, but after this point, a sudden liberation of copper into the blood stream may occur, resulting in extensive haemolysis, jaundice and death. Susceptibility to cumulative copper poisoning varies with the species and the individual, but of all farm stock, sheep seem to be the most susceptible. Bovines from six months of age and upward have a fairly high resistance (Cunningham, 1946) but young calves can readily store dangerous amounts of copper when small quantities are added to the food (Shand and Lewis, 1957).

Before Boughton and Hardy (1934) described chronic copper poisoning in sheep due to ingestion of excessive amounts of a copperized salt lick, the condition had been reported only infrequently and incompletely. The most comprehensive investigation of this condition has been carried out by Australian workers (Albiston *et al.*, 1940; Bull, 1951; Bull *et al.*, 1956) in connection with the occurrence of chronic copper poisoning in grazing sheep in Australia. Bull (1951) has described its occurrence there under three different field conditions: (1) when the copper contents of soil and herbage are high, as on cupriferous soils, (2) when both these are within the normal range and (3) in association with liver damage due to poisoning by the plant *Heliotropium europaeum*, abundant growth of which occurs in summer pastures on certain areas under favourable weather conditions. Under (1) the condition is associated with a straightforward high intake of copper due to the high

copper content of the pastures and by their contamination with cupriferous soil Some plant species in these areas have shown copper concentrations up to 50–60 p p m There is no seasonal incidence and deaths from chronic copper poisoning occur in every month of the year The condition under (2) is usually seasonal in occurrence, the incidence is much higher in British breeds or crosses than in Merinos, and is associated with a dominant pasture growth of subterranean clover (*Trifolium subterraneum*) which commonly contains 10–15 p p m copper, but very low levels of molybdenum, usually less than 0 1 p p m. The evidence suggests that the actual intake of copper, and the copper molybdenum ratio are important factors in the development of the disease That other factors are also involved is strongly supported by the pen-feeding experiments of Dick (1956) which have demonstrated the significance of the inorganic sulphate content of the diet The disease associated with the consumption of *H europaeum* i.e condition (3), has been shown (Bull *et al*, 1956) to be due essentially to the altered metabolism of the liver cell resulting in an atrophic hepatosis Excessive storage of copper occurs—usually 1,000–2,000 p p m or more and the liver damage predisposes sheep to the haemolytic crisis of chronic copper poisoning

Bull (1951) has reported that there appears to be no malnutrition associated with any of these types and has characterized the condition as a more or less sudden haemoglobinaemia and haemoglobinuria, usually with icterus, necrosis of the liver, kidney dysfunction and so-called 'uraemia' are associated with the haemolytic crisis The liver copper concentration is usually higher than 1,000 p p m, but an abnormally high liver value cannot be taken as proof of copper poisoning unless the other characteristic pathological effects are also present Under Australian field conditions the haemolytic crisis is commonly precipitated by a falling plane of nutrition, by fasting associated with movement or handling of stock or by further assimilation of copper, when the liver copper concentration is already high

In Britain outbreaks of chronic copper poisoning in sheep, associated with grazing in orchards where horticultural copper sprays were used, have been reported by Fincham (1945) and Ogilvie (1954) Weybridge records show that its occurrence under these conditions is much more frequent than published reports indicate, and confirm Boughton and Hardy's 1934 observation that the fatal haemolytic crisis can occur some months after the sheep have been removed from the source of extraneous copper, the precipitating factors being a falling plane of

nutrition or other physiological stresses. Recent reports of other outbreaks have been connected with the feeding of copperized mineral supplements to sheep receiving a concentrate ration (Clegg, 1956; Pearson, 1956; Peggie, unpublished data).

These cases fall under the first set of conditions described by Bull (1951) and because of the widespread use of mineral mixtures in this country, it is important to focus attention on them. A case which falls under the second set of conditions, i.e. chronic copper poisoning associated with a 'normal' copper concentration of the food, occurred in a group of eight stalled sheep at Weybridge fed for about 3 years on hay and a concentrate mixture containing 12 p.p.m. copper, 1·1 p.p.m. molybdenum and 0·7 per cent inorganic sulphate—concentrations which are regarded as normal for such a ration. The sheep were accidentally subjected to some sudden and unaccustomed exercise, within 24 hours of which there were two clinical cases of typical chronic copper poisoning with liver values of 1,000–3,000 p.p.m. On slaughter two other animals showed liver copper concentrations of about 1,000 p.p.m.

In another group of six sheep maintained on a similar diet for 2·5 years, liver copper values of 1,000–2,000 p.p.m. were found, but these sheep were not subjected to any nutritional or physical stress before slaughter and no copper-poisoning symptoms occurred. In both these cases the molybdenum content of the diet was within the 'normal' range and much higher than that of the pastures on which chronic poisoning occurs in Australia (1949). The inorganic sulphate content was also high and according to Dick's findings should have been ample to allow the molybdenum to exert its full limiting effect on liver copper storage.

More recently deaths in sheep, from about four months of age onwards, have been associated with proprietary pelleted concentrate rations containing copper within the limits thought to be safe (Lewis and Allcroft, unpublished data). A revision of ideas on what constitutes a safe limit, particularly for sheep, is necessary. Until results of experimental work allow a more exact definition of the copper requirements of sheep under different dietary regimes, the potentially toxic effect of too high a concentration of copper in the food should be emphasized.

Cattle appear to be more resistant than sheep to repeated doses of copper sulphate. Cunningham (1952) observed no ill effects from feeding two growing calves, seven months old at the beginning of the

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Cattle appear to be more resistant than sheep to repeated doses of copper sulphate. Cunningham (1952) observed no ill effects from feeding two growing calves, seven months old at the beginning of the

experiment, and two adult cows, 0 8–5 gm copper sulphate daily for nine months or longer Kidder (1949), however, produced chronic copper poisoning and death in a steer after about four months on a daily drench of 5 gm copper sulphate More recent evidence indicates that copper poisoning in cattle, especially in young calves, occurs more frequently than has hitherto been suspected Deaths in young calves approximately 2–4 months of age which were reared on commercial milk substitutes to which small amounts of copper had been added to bring the total copper content to 60–100 p p m were attributed to excessive accumulation of copper (Shand and Lewis, 1957) It is of interest that relatively small additions of copper to the food of the young calf can result in such a rapid and dangerous increase in liver copper during the period when normally there is a decline in liver copper concentration

Acute copper poisoning is not common, but cases have been recorded as a result of accidental overdosage or access to sources of copper compounds The symptoms and lesions are quite distinct from chronic or cumulative copper poisoning and blood and liver copper levels are not always abnormally increased after single lethal doses

CONCLUSION

From this account of the copper-deficiency syndromes and also of copper poisoning, it will be evident that copper metabolism in sheep and cattle is a complex physiological function which is as yet incompletely understood Under some circumstances the occurrence of chronic copper poisoning in sheep is just as paradoxical as the development of copper deficiency This is illustrated by the occurrence of severe copper deficiency in cattle on a farm where pasture copper values range from 15 to 50 p p m.—a range similar to that in which copper poisoning occurs in sheep in Australia Swayback has occurred frequently on a farm with pasture containing copper, molybdenum and inorganic sulphate values in the region of 12 p p m., 1 p p m. and 0 7 gm per cent respectively, whereas chronic copper poisoning developed in stalled sheep on a diet supplying similar concentrations of these constituents (Allcroft and Lewis 1957) As yet our knowledge of the factors concerned is not sufficient to explain the existing complexities

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CHAPTER TWENTY-SIX

Cobalt Deficiency

H J LEE

Introduction—Distribution—Cobalt-deficient soils—Manifestation and incidence—Requirements and function—Content of pastures and of liver—Diagnosis—Control—Cobalt in other disease conditions

For centuries, animal husbandmen in many parts of the world have been puzzled by a wasting malady that has complicated the care of their flocks and herds in certain restricted localities Their animals would gradually lose condition and eventually die if they were confined too long to the seemingly adequate pastures in these areas The descriptions of the wasting diseases that plagued these flocks and herds, in several countries of the New World as well as the Old, had many points of similarity and it came to be recognized that a common cause was probably responsible for all of them All manner of reasons were put forward, from time to time, to explain these maladies in the light of current knowledge or superstition. In the more distant past legend had it that a mystical curse (The Evil Spirit breathe death upon your cattle !) was responsible in some instances, in others, 'a miasma from the sea' was considered to be the cause More prosaically, in comparatively recent times, the condition has been attributed variously to the ingestion of toxic plants, to the ravages of parasitic infestation to a lack of phosphorus in the herbage, or to an imbalance of major mineral nutrients These hypotheses have all been found to be untenable when subjected to critical investigation

More than fifty years ago at the turn of the century, the lack of an essential nutrient in the soil of the affected localities came to be sus-

pected in New Zealand and this led, eventually, to the earliest successful therapeutic treatment. There, a logical attempt was made to alleviate, by means of iron preparations, the profound anaemia that commonly developed in animals seriously affected by Bush Sickness. Massive doses of commercial iron salts, or of iron-rich compounds from certain naturally occurring ore deposits, were found to exert a decidedly beneficial influence on the general condition of the animals as well as on the accompanying anaemia. In accord with these observations a theory was advanced that this manifest improvement was due to the correction of an iron deficiency (see Aston, 1924). Further investigation in Western Australia, however, revealed that chemically pure iron compounds were of no therapeutic value, even when given in large amounts, and that the virtue of the effective compounds lay solely in the impurities they contained (Filmer and Underwood, 1934).

Nevertheless, the mystery that for so long attached to this widespread group of wasting diseases was not finally dispelled until the solution was provided to one of these maladies in South Australia. There, sheep that were confined for more than a few months to certain coastal tracts invariably lost condition progressively and ultimately died of Coast Disease. Intensive investigation proved this disease to be due primarily to a relative lack of cobalt in the grasses that flourished in those regions (Lines, 1935; Marston, 1935) complicated by a secondary lack of copper. Coast Disease could be completely prevented or overcome by providing the animals with an adequate supplement of cobalt and copper, but not with copper alone. This was the first demonstration that cobalt played an essential role in any normal physiological process.

Shortly after this discovery was announced, the active impurity responsible for the efficacy of the curative iron compounds was shown, in fact, to be cobalt. The recognition that many of the related wasting diseases in other parts of the world were also due to cobalt deficiency soon followed. Means of correcting cobalt deficiency in practice were devised and these have been subjected to modification and improvement ever since. As a consequence, an extensive literature has been built up over the past two decades which covers the description of cobalt deficiency as it occurs in a wide range of circumstances, the corrective measures adopted to meet these circumstances and, ultimately, the explanation of the primary function of cobalt in ruminant nutrition. This literature has been reviewed by several authors so reference is made in this chapter to relatively few

publications, in particular to some that have appeared since the relevant reviews were written.

Of the more recent reviews the reader is referred to Beeson (1950) for a survey that deals, particularly, with the relationship of the concentration of cobalt in the soil and in pasture plants to the grazing animal; to Marston (1952) for a comprehensive consideration of all aspects of the physiology of cobalt; to Hopkirk and Patterson (1954) for some early historical references, together with an account of the 'iron starvation theory'; to Young (1956) for a review of some of the geochemical, analytical and biochemical aspects of cobalt nutrition; and to Underwood (1956) for a general survey of this field.

DISTRIBUTION

In Australia, the occurrence of Coast Disease (a dual deficiency of cobalt and copper) in sheep and, to a lesser extent, in cattle is restricted to the areas adjacent to the southern seaboard in Western Australia, South Australia, Victoria and Tasmania. Enzootic Marasmus or Denmark Disease in cattle in Western Australia is also due to cobalt deficiency, and a seemingly identical condition in sheep in central Queensland responds to cobalt therapy.

Bush Sickness in sheep and cattle in New Zealand occurs in several localities in both the North Island and South Island; in the South Island a similar condition is also referred to as Mortons Mains Disease.

Cobalt deficiency is widespread in the British Isles where sheep, particularly, have suffered. It has been recognized in the islands of the Hebrides and the Orkneys and has proved to be the cause of 'Daising' or 'Vinquish' in Ayrshire and of 'Pine' in several other counties in the north and west of Scotland. Border Pine and Northumbrian Pine occur in the Cheviot Hills on the Scottish border but most of the cobalt-deficient areas in England are in the south-western counties. There Pining occurs in Herefordshire, Worcestershire, Cornwall and Devon; in Devon, the 'Moor Cling' of Dartmoor is also due to cobalt deficiency. In Wales, Eire ('Summer Pine' in sheep and 'Galra Thrua' in cattle) and in Northern Ireland cobalt deficiency has been identified in several counties.

Both lambs and calves have suffered from cobalt deficiency in Norway ('Dry Sickness', 'Drought Disease') especially in the coastal regions; and the deficiency syndrome has been recognized in cattle in Denmark, Sweden ('Mossjuka', 'Moor Disease'), Estonia, Latvia ('Bog

Disease') and possibly in Finland. The same condition has been reported in sheep in Poland, in sheep and cattle in the U.S.S.R., and in calves in Germany, Austria, Holland and Spain ('Sequeira' or 'Dry Sickness'). Certain districts in Greece and Turkey are also suspect and 'No Eating Disease' ('Kuwazu') in Japanese cattle may well be due to cobalt deficiency.

On the Atlantic coast of North America, the disabilities imposed by cobalt deficiency have been widely recognized, particularly in cattle, in the Canadian province of Nova Scotia and in New Hampshire ('Burton Ail'), Massachusetts ('Neck Ail'), New Jersey, Delaware, Virginia, North and South Carolina and Florida ('Salt Sickness') in the United States. The deficiency probably exists also in the northern part of New York State and in states as far apart as Oregon in the west and Arkansas and Louisiana in the south. In the vicinity of the Great Lakes, the same condition has been identified in Michigan and Wisconsin and possibly, in Illinois ('Lake Shore Disease', 'Grand Traverse Disease'); and in Ontario, Canada. In western Canada, sheep have also been affected in Alberta and possibly in Saskatchewan.

An identical disease has been reported to cause mortality in cattle in the Brazilian State of São Paulo, where it is referred to by a number of descriptive names ('Dry Disease', 'Sand Sickness', etc.).

In Africa, both sheep and cattle may suffer from cobalt deficiency in Kenya ('Nakuruitis') and in the coastal region of western Cape Province, while cobalt supplements are recommended for grazing stock in the Congo, also.

It is highly probable that cobalt deficiency adversely affects the health of ruminants in many other areas that have yet to be recognized.

In several countries maps have been prepared which indicate the distribution of the cobalt-deficient areas. This has been done in Scotland (Stewart, Mitchell, Stewart and Young, 1946), part of south-western England (Osborne, Featherstone and Herdan, 1954), Denmark (Schambye and Jacobsen, 1955), the United States of America (Beeson, 1945; Thacker and Beeson, 1958), South Australia (Lee, 1951), Western Australia (Harvey, 1937; Bennetts, 1955), Tasmania (Green, 1956) and New Zealand (Andrews, 1956).

COBALT-DEFICIENT SOILS

Cobalt deficiency in ruminants has been associated with a diversity of soil types. Highly calcareous shell sands have proved to be deficient

in the extreme, while the soils that have formed as a result of the consolidation and weathering of such parent material are also deficient, though less profoundly These derived soils range from leached siliceous sand, on the one hand, to heavy black clay (rendzina) on the other Granites and other igneous intrusions, as well as volcanic lava and pumice showers, have commonly given rise to deficient soils Cobalt deficiency has also occurred on such widely different soils as forest loam, peat and those derived from sandstone and glacial loess

It is clear that any soil from which insufficient cobalt may be absorbed by the fodder plants to satisfy the requirements of the grazing animal must be classed as cobalt deficient This state is determined in the first place by the cobalt content of the parent material, later by the modification that this material has undergone during the process of soil formation (which may involve the concentration, the dilution or the removal of cobalt), and, finally, by the availability to the growing plant of the form in which the cobalt occurs in the soil The availability depends upon climatic and other factors that are not completely understood and, in some soils, may vary markedly from season to season, there can be no close correlation, therefore, between the total amount of cobalt in the soil and the appearance of cobalt-deficiency symptoms in grazing stock. As a guide, however, a level of approximately 5 p p m. cobalt in the soil may represent the limit below which the malady can be expected to occur in most seasons

A closer correlation has been claimed to exist between the condition of the animals and the amount of cobalt that may be extracted from the soil by 2 5 per cent acetic acid According to this claim, soils from which less than 0 25 p p m cobalt may be extracted by this means are likely to be associated with cobalt deficiency in sheep and cattle

MANIFESTATION AND INCIDENCE

Cobalt deficiency is essentially a progressive wasting disease which, in its extreme form, invariably proves fatal Only ruminants are affected, consequently, the disease has been observed most commonly in sheep and cattle and, less frequently, in goats The deficiency syndrome is similar in sheep and cattle although sheep are, generally, the more readily affected Lambs and calves are more susceptible than the mature animals and it is by no means unusual to encounter a fatal deficiency in the young while their dams appear to be in full thrift. The appetite of sheep confined to grossly deficient pastures fails

progressively. The animals become increasingly weak and lethargic as they gradually lose weight. Wool growth is seriously impaired; the fleece becomes tender and appears dull and lifeless. A profound anaemia becomes apparent in the blanched mucous membranes of the eyelids, muzzle and mouth. The eyes are dull and rheumy and the wool on the face is matted by an excessive exudation of tears; the ears droop and the deficient sheep presents a picture of bleary-eyed dejection; in the terminal stages the pale, parchment-like skin becomes extremely fragile before the animal dies in an emaciated state.

The appearance at post-mortem of the carcass of a sheep that has died of cobalt deficiency does not differ markedly from that of one which has succumbed to prolonged semi-starvation; there is a complete absence of fat, extensive oedema is a usual feature and fragility of the bones is common. There are no gross changes incompatible with a picture of general malnutrition.

When a profound deficiency of this nature prevails, adult cattle also lose weight steadily. Their hair coats become rough and unkempt, anaemia develops and a capricious pica is frequently associated with progressive inappetence. The cows' milk production fails so the calves starve and, if the deficiency is not relieved, the cows themselves will die.

The severity of the manifestations encountered, as well as the course of the disease, are governed by the degree of the deficiency. On pastures where a deficiency less profound than that described in the preceding paragraphs consistently prevails, mature sheep and cattle are seldom affected seriously and mortality is rare in this age group. Their progeny, nevertheless, either fail to grow normally—sometimes without showing specific signs—or they waste and die. Under these circumstances anaemia is nor a constant feature of the malady.

In certain deficient localities, the incidence of the disease from year to year is unpredictable and highly erratic. Under these circumstances, the manifestations of deficiency that do show in the flock or herd are extremely variable. The experience with a Romney Marsh flock that was maintained under experimental conditions on incipiently cobalt-deficient terrain in South Australia during fourteen consecutive years may be quoted as an example. Half of these ewes, their replacements, and their progeny were dosed regularly with cobalt and remained healthy throughout this considerable period. These sheep provided a striking contrast for the behaviour of the comparable ewes and lambs which received no cobalt supplements. In four of these fourteen

years, the untreated lambs suffered mortalities that ranged from 30 per cent to 100 per cent of the total lamb crop. In two other seasons the lambs from the untreated ewes were markedly unthrifty, they showed many of the signs of cobalt deficiency but none of them died. The growth rate of the lambs was retarded slightly but significantly during three further years, these lambs appeared healthy and the mild degree of deficiency was clinically detectable only by comparison with the heavier, better-grown lambs that were dosed with cobalt During the remaining five years, there was no detectable difference between the treated and the untreated lambs The sequence of the years in which these different degrees of deficiency were observed was completely random The untreated ewes suffered during only one of these fourteen years at a time when, for the second successive year, their lambs were grossly affected, then the ewes lost weight steadily and several of them died of the typical cobalt-deficiency syndrome

The untoward signs of cobalt deficiency are closely bound up with the progressive loss of appetite that supervenes when the amount of cobalt ingested is insufficient to provide the animal's requirement There is no loss of ability to digest normally the food that is consumed A record of the food intake of a sheep restricted to a cobalt-deficient diet reveals a close parallel between the amount consumed and the body weight of the animal As the intake decreases so does the weight decline but, when an adequate supplement of cobalt is provided for the deficient animal, appetite recovers sharply and a general improvement in the condition of the animal is soon apparent Anaemia, when this is present, responds more slowly

Cobalt-deficient animals in any but the last stages of the malady may be restored to normal health by adequate cobalt therapy

pastures. The upper limit of this range undoubtedly provides a considerable margin of safety, for a pasture that supports healthy sheep will maintain cattle equally well. It is probable, therefore, that approximately 3–4 mg. each day are sufficient for cattle.

For some years after the importance of cobalt in ruminant nutrition was clearly established, its precise function within the paunch remained a mystery. In 1948 it was discovered that the newly isolated anti-pernicious anaemia factor, vitamin B_{12}, contained about 4 per cent of cobalt as an integral constituent of this crystalline product and, as a result of this discovery, the search for the function of cobalt in ruminants was intensified. It was found that the intramuscular injection of sufficient quantities of vitamin B_{12} would alleviate all the symptoms of extreme cobalt deficiency. The daily injection of 6 μg. of the vitamin was found to maintain sheep restricted to a cobalt-deficient diet in robust health, although considerably larger doses are required to effect recovery in deficient animals. Relatively huge amounts must be given by mouth to achieve the same result. Vitamin B_{12} is elaborated only by micro-organisms and the sole function of ingested cobalt appears to be to ensure that certain of the micro-organisms which normally inhabit the rumen are provided with an adequate substrate for the production of the vitamin. It is evident that a very considerable excess of vitamin B_{12} must be produced in the rumen, for only a relatively small proportion of the total amount elaborated is absorbed: A still smaller proportion is stored in the tissues, principally in the liver. The cobalt-deficiency syndrome and most of the observations related to it may be adequately explained in the light of these facts (Marston, 1956).

An animal whose cobalt intake is adequate is able to produce sufficient vitamin B_{12} to satisfy its immediate requirements and to build up a reserve in the liver and other tissues. When the amount of cobalt ingested falls below the minimal requirement the population structure of the rumen flora changes. The quantitative relationship between the various micro-organisms undergoes drastic modification as certain of them disappear and others, that usually constitute a relatively small proportion of the total, predominate. Concurrently with these changes the production of vitamin B_{12} falls off sharply. When this happens, the animal is able to satisfy its needs only by drawing from the accumulated store of vitamin B_{12}, and the period during which this will suffice is limited by the extent of the reserve. Signs of deficiency will not develop until this reserve is exhausted. A sheep may thus remain

in perfect health during an interval when the pastures are cobalt deficient so long as its previous grazing history has enabled it to store an amount of vitamin B_{12} sufficient to make good the deficit.

On the other hand the lamb or calf which is born on cobalt-deficient pasture, or restricted to a deficient diet early in life, has little opportunity to accumulate vitamin B_{12} and the reserves with which it is born are soon depleted The requirements for growth impose additional stringency in the young animal It is therefore apparent why adult animals with adequate reserves and a relatively small requirement of vitamin B_{12} are able to withstand a lack of cobalt which may prove fatal to their young with meagre reserves and a greater requirement It becomes clear also why cobalt that is stored in the tissues other than that which is incorporated in vitamin B_{12} serves no useful purpose This stored cobalt cannot relieve cobalt deficiency for no physiological mechanism exists for the transfer of cobalt from the tissues to the rumen where the effective synthesis of vitamin B_{12} takes place

Legumes generally contain a greater proportion of cobalt than do grasses or cereals grown in the same soil and this discrepancy may at times be very considerable. As an example, in South Australia, lucerne (*Medicago sativa*) frequently contains more than 0·3 p.p.m. cobalt, while the perennial grass *Phalaris tuberosa* collected at the same time from the same pasture contains less than 0·03 p.p.m. Under these circumstances, the influence of the season or other factors on the botanical composition of the pasture may frequently determine the cobalt status of the grazing ruminant and, at times, account directly for the variable incidence of cobalt deficiency. The animals are bound to suffer most severely when the availability of cobalt even to the leguminous plants is inadequate, as is not uncommonly the case.

DIAGNOSIS

The response of the animal to supplementary cobalt—that is, the improvement in appetite, in body weight and in general thrift—is by far the most certain method of diagnosing cobalt deficiency. When animals suspected to be suffering from cobalt deficiency are dosed or otherwise provided with cobalt for this purpose, it is desirable that the behaviour of an adequate number of untreated animals, maintained under comparable conditions, should be observed simultaneously in order that the response to the treatment may be assessed objectively. When practical difficulties preclude such a comparison, however, reliance must be placed on analytical procedures as an alternative means of diagnosis. Opinions differ as to which of these analytical procedures is most reliable and the choice must depend to a large extent on the facilities available and more particularly on the ability, born of experience, to interpret the findings.

An analysis of the soil will frequently serve to confirm suspected cobalt deficiency or to indicate where deficiency is likely to occur, and the concentration of cobalt in the pasture and in the liver provide an extremely valuable indication of the cobalt status of the animal. When the results obtained by any one of these procedures are very low or particularly high, they may be accepted with confidence as evidence for or against the existence of cobalt deficiency. Many of these figures, however, will be found to be intermediate between these extremes and may only be interpreted after a careful consideration of the state of the animals and their grazing history.

A gross state of deficiency may be recognized readily, for the

response of the sickly animals to cobalt therapy will be dramatic and the levels of cobalt detectable in the soil, the pasture and the liver will be very low A slight degree of deficiency, on the other hand, presents a far more difficult problem Prolonged objective measurements will probably be necessary to detect the response to cobalt supplementation and the analytical findings may frequently be equivocal There is every promise that the microbiological assay of vitamin B_{12} in the blood plasma or, more particularly, in the liver may prove to be an exceptionally useful method of diagnosis Blood plasma is readily obtainable but, as the concentration of vitamin B_{12} in this medium is subject to considerable short-term fluctuations, the more stable reserves in the liver afford a much better assessment of the vitamin B_{12} status of the animal A small sample of liver drawn at biopsy from an intact animal supplies ample tissue for the assay

The livers of sheep on healthy pastures have been found to contain about 1 μg vitamin B_{12} per gramme of fresh tissue, while a similar figure for cobalt-deficient sheep is usually below 0 1 μg /gm The blood plasma of the normal sheep contains from 3 to 6 mμg B_{12}/ml and this value falls below 0 3 mμg /ml in the deficient animal (Dawbarn, Hine and Smith, 1957) The possible application of these findings has not been fully worked out as yet, but the procedure should find favour in veterinary and biological laboratories where the intricacies of trace element analysis present difficulties

the locality where the trouble arose and, when the distances were too great, the attractive pastures that provoked pining were reluctantly abandoned. In any case, the necessity to transfer stock to and fro was an irksome and inefficient procedure and was sometimes impossible because of the restrictions imposed by land tenure.

Following the discovery of the common cause of these wasting diseases and of means of overcoming the deficiency of cobalt, the forced movement of the flocks and herds became unnecessary. Sales were no longer dictated by the fear that the stock would deteriorate if held longer in the deficient areas, but were determined by ordinary farming practice. The appropriate treatment of the animals themselves or of the deficient pastures they graze has made possible a more stable and economically sound system of husbandry; and has enabled areas that had been abandoned because the hazard was too great to be brought back into production.

Of the procedures commonly adopted to correct cobalt deficiency, no one method can have universal application, for the condition may arise in almost as many circumstances as there are methods of husbandry. For instance, in many parts of Europe and North America animals may spend almost half their lives in barns while in Australia and some other countries, they are never housed. A different approach to the problem of providing supplementary cobalt will be necessary in each case. Further, the procedure which is both practicable and economically sound on a few Irish acres may not be equally acceptable on a Scottish hill grazing or an open prairie in Alberta; and the method which suits a compact, highly developed farm carrying five or six breeding ewes per acre may not find favour in large tracts of low-carrying capacity, particularly in rugged country which is difficult of access. The erratic incidence of the disease in some localities further complicates the choice.

In cobalt-deficient regions, any method of cobalt supplementation which enables the vitamin B_{12} status of the animals to be maintained adequately is effective. The method best suited to the circumstances that exist in each locality must be determined and applied. This objective may be achieved by ensuring the daily ingestion of sufficient cobalt to provide the requirements of vitamin B_{12} from day to day, or the less frequent consumption of larger amounts of cobalt, each of which will permit the elaboration and storage of sufficient vitamin to supply the animal's needs until additional cobalt is made available once more. Fortunately, ruminants tolerate relatively huge doses of

cobalt, so that the risk of poisoning with cobalt supplements is negligible

For the sheep, a sufficient daily consumption is about 0 1 mg Co but a very much greater daily equivalent is required when the cobalt supplements are provided only at infrequent intervals Sheep on pastures that are grossly cobalt-deficient can be maintained indefinitely in perfect health if they are dosed with 7 mg Co at weekly intervals but, with 21 mg Co at intervals of three weeks, they gradually lose condition and with 35 mg Co once every five weeks they will die, they will succumb less rapidly than sheep receiving no cobalt supplements, but just as certainly It would appear that the rumen organisms are unable to convert large doses of cobalt to vitamin B_{12} efficiently, or that the mechanism for adsorption and storage cannot cope with a suddenly enhanced but brief production of vitamin B_{12} When the interval between doses is four weeks, as much as 280 mg Co must be administered on each occasion to maintain the mature sheep Even with this amount of cobalt, young sheep do not thrive When the pastures are less deficient, however, the amount of cobalt ingested in the grazing is somewhat greater, so the animal s total requirement for vitamin B_{12} is not greatly in excess of the amount derived from the rumen In this case, any storage of vitamin B_{12} that results from cobalt supplementation will be drawn on but slowly and in small amounts, so that relatively large, infrequent supplements of cobalt will maintain the health of ruminants much more efficiently on mildly deficient than on grossly deficient rations

Dosing individual animals frequently with cobalt is a positive means of correcting cobalt deficiency which is effectively employed in some circumstances but, because of the considerable labour involved this procedure does not find widespread favour Salt licks or fodder supplements that are made available for sheep or cattle continuously or at frequent intervals may be used as vehicles for cobalt supplements A solution in water of the soluble cobalt salt, calculated to provide the required supplement, is best sprinkled over the salt or fodder to ensure an even distribution Even so the amount of cobalt to be used can only be calculated on the assumption that the supplement will be equally consumed by all the members of the flock or herd to be protected. Actually, individual appetites vary considerably and some animals which do not take enough of the supplement will suffer the consequences Nevertheless, this method is rather widely employed and meets with the greatest measure of success when it is used in con-

junction with a programme of occasional drenches for the relatively few animals that do show signs of cobalt deficiency.

In some deficient localities, practical farmers have attempted to maintain a corrective concentration of cobalt in the stock watet supply, despite the disadvantages inherent in this practice. Cobalt solutions will attack most types of metal reservoirs and drinking troughs and may not, therefore, be left in prolonged contact with them. A further disadvantage is that the cobalt is thrown out of solution when carbonates are present in the water and may be lost to the animals in this way. To assess the dose rate accurately under these circumstances is impossible. Sheep at pasture seldom drink when the grass is succulent and the weather is cool whereas ready access to water is a constant necessity during hot weather, particularly if the pasture is dry. Under these circumstances, sheep that graze the green, cobalt-deficient pasture may be entirely dependent on the reserves of vitamin B_{12} they have been able to accumulate during the hot months. These reserves are seldom adequate. Cattle are likely to be better served by this procedure as they drink in all seasons.

So far as is known, cobalt is not an essential element for plant growth* and may even exert a deleterious effect if it is present in excess. However, when it is present in the soil in an available form, cobalt is absorbed by the roots and distributed throughout the plant to an extent that appears to be limited largely by the availability of the supply, for grasses grown in water culture supplied with cobalt may absorb more than fifty times their usual concentration of this element. It has been pointed out earlier that the various plant species differ markedly in their inherent propensity for taking up cobalt from the soil in which they grow and that legumes almost invariably absorb more cobalt than do grasses. When cobalt is applied to cobalt-deficient pastures, however, additional cobalt is absorbed by all types of plants. When the concentration is raised sufficiently by this means, the ingestion of an adequate amount of cobalt by all the grazing animals is assured. The effective simplicity of this practice has led to its widespread adoption.

Cobalt sulphate usually constitutes the source of cobalt for applica-

* Recent work at Berkeley, California, has convincingly demonstrated that cobalt is essential for the fixation of nitrogen in the root nodules of legumes grown in artificial media (Reisenauer, 1960), and Powrie (1960), has reported a significant response by *Trifolium subterraneum* to cobalt applied to a poor, sandy soil in South Australia.

tion to deficient pastures and to ensure its even distribution this salt is commonly mixed with a carrier such as superphosphate or other fertilizer for spreading Inert materials such as sand are sometimes used for this purpose while, recently, aqueous solutions of cobalt sulphate have been sprayed on the deficient pastures with considerable success. This last procedure is particularly well adapted for spraying inaccessible hilly country from low-flying aircraft The concentration of cobalt in pastures or on the surface of the plants (where it is equally effective) is greatest shortly after the cobalt sulphate has been spread Thereafter, this concentration falls steadily until the pastures once more fail to provide sufficient cobalt for the animals When this happens, the application must be repeated and a great deal of experimental work has been carried out to determine the necessary rate and frequency of application to overcome cobalt deficiency in different circumstances For example, in Great Britain the application of 2 lb of cobalt sulphate per acre every fourth or fifth year has proved to be effective and well adapted to the existing rotational cropping practice In New Zealand, on the other hand, the annual application of 4–5 oz per acre to the permanent pastures has commonly been adopted, while 16–20 oz every third year has also been found to be satisfactory

However, in localities where the incidence of cobalt deficiency is sporadic the intervals between deficient periods may be several years and, in these areas, the relatively short-lived elevation of the cobalt concentration in the pasture that results from the application of cobalt sulphate may make this corrective procedure economically unattractive There would be many years when neither increased productivity nor improved financial return would be achieved

One curious effect of applying cobalt to a deficient pasture is to render it more attractive to grazing sheep This has been strikingly demonstrated on Scottish hill grazings where strips of pasture treated with cobalt sulphate were alternated with strips left untreated (Stewart, 1953) The sheep consistently preferred the cobalt-treated pasture strips No satisfactory explanation of this phenomenon has been offered. It would appear to be advisable, therefore, to spread the cobalt dressing evenly in order to avoid over-grazing the more palatable sections

Where rotational grazing is practicable but the application of cobalt to the entire property is not feasible, the frequent application of relatively heavy dressings to at least one enclosure is worthy of consideration The ingestion of this cobalt-enriched pasture will enable the

animals which are confined to it periodically for limited intervals to store sufficient vitamin B_{12} to maintain them while they graze the deficient sections of the property.

It appears probable that, before long, all these methods of overcoming cobalt deficiency may be superseded by a recent development that involves an entirely new principle. Recent research at the Division of Biochemistry and General Nutrition of the Commonwealth Scientific and Industrial Research Organization in South Australia (Dewey, Lee and Marston, 1958) has revealed that cobaltic oxide, a relatively insoluble source of cobalt, may be compounded with inert material such as china clay or finely divided iron into a dense pellet that will remain intact within the reticulum of the sheep for many months. A small but adequate quantity of cobalt passes continuously from this source into solution in the rumen fluid to provide enough for the animal's requirement for a considerable period. The length of time for which a single pellet, weighing only a few grammes, may remain effective in the rumen has not yet been determined but the stimulating possibility is that one treatment may be all that is necessary to satisfy the animal's demand for vitamin B_{12} throughout its lifespan. If this proves to be the case, or even if the effective life of the pellet is considerably less, this method may be expected to find widespread acceptance as it should be suited equally to all of the circumstances under which cobalt deficiency prevails.

COBALT IN OTHER DISEASE CONDITIONS

PHALARIS STAGGERS IN SHEEP AND CATTLE

Phalaris tuberosa is a perennial grass of Mediterranean origin which is extensively used in sown pastures in southern Australia and, less commonly, in certain districts in the South Island of New Zealand. It is grown, also, to a limited extent in Chile, Uruguay and Argentina, in some districts in California and in South Africa, but in these countries it is at present only of minor importance as a pasture plant. Phalaris is admirably suited to all of these environments except that, in many circumstances, it contains a neurotoxic substance when it is actively growing. Sheep or cattle that consume sufficient of the toxic phalaris consistently during two or three consecutive weeks, which they may do when the grass is predominant in the pasture, commonly develop a malady known as Phalaris Staggers (McDonald, 1942). This condition, which is frequently fatal and may at times occasion heavy losses,

has been reported to occur only in Australia and New Zealand. During 1956 and 1957, however, a seemingly identical disease was recognized in Southern Rhodesia on irrigated pastures that consisted essentially of Ronpba grass, a hybrid of *Phalaris tuberosa* and *Phalaris arundinacea* (Croft, personal communication). More recently still a similarly named *Phalaris* hybrid has proved to be toxic in Florida also, (Ruelke *et al.* 1961).

In recent years, experimental investigation of Phalaris Staggers has proved conclusively that the syndrome may be prevented entirely if sufficient cobalt is ingested simultaneously with the phalaris (Lee and Kuebel, 1953). This subject has been reviewed by Lee (1956).

There is no point of similarity between Phalaris Staggers and uncomplicated cobalt deficiency, apart from the preventive role played by cobalt within the paunch. The nervous manifestations that are the principal feature of Phalaris Staggers are never encountered in cobalt-deficient animals that have no access to phalaris. Sheep or cattle are usually in excellent condition when affected by staggers and there is no progressive loss of weight. The onset of the disease is rapid and, furthermore, its course cannot be arrested by cobalt therapy. The nature of the toxic substance present in the phalaris has not been determined.

The function of cobalt in preventing staggers is not yet known, but it has been proved that the production of vitamin B_{12} is not involved, for massive injection of this vitamin will neither prevent nor alleviate the condition. It is therefore evident that, in this disease at least, cobalt has an additional part to play in ruminant nutrition.

OTHER DISEASES

Claims have been made that cobalt supplements may be of benefit, also, in several other conditions which do not involve an ordinary lack of cobalt. For instance, the appetite and the general health of cattle affected by diseases as dissimilar as ketosis and malignant catarrh appear to respond to therapeutic doses of cobalt, while the addition of cobalt to the rations apparently enhances the growth rate of pigs. The function of cobalt in these conditions has not been determined.

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CHAPTER TWENTY-SEVEN

Iodine

G. CALDERBANK

Introduction—Natural sources of iodine: in soil and water, in pasture, intake by grazing animals—Iodine metabolism: in the thyroid gland, in blood, in milk—Thyroid function: growth, milk yield, milk quality, wool production, reproduction—Thyroid dysfunction—goitre, causes, occurrence and distribution, symptoms and diagnosis—Control of iodine deficiency: iodine requirements, toxicity, practical considerations.

Iodine is one of the scarcest of non-metallic elements although it is almost universal in its animal, vegetable and mineral distribution. It is found in quantity only in some forms of marine life; in certain deep well waters and mineral springs; and in the natural deposits of *caliche* in northern Chile from which the greater part of the world's commercial supply is derived.

The discovery of iodine was made near Paris towards the end of 1811 or early in 1812 by Courtois who accidentally caused the liberation of violet-coloured iodine vapour from the residue of seaweed ash used in the manufacture of saltpetre; and in 1813 the new element was named 'iode' by Gay-Lussac and thence 'iodine' by Humphry Davy. Early investigations, notably by Chatin, associating the incidence of human goitre with iodine deficiency, unfortunately suffered from certain discrepancies and as a result were largely discredited. Although later work re-established the connection between iodine deficiency and goitre, little further progress was in fact made until in 1891 Murray showed that myxoedema could be relieved by injections of thyroid extract, and in 1895 Baumann demonstrated the presence of iodine in the thyroid gland. These findings awakened new interest, and subsequent research culminated in the isolation of the iodine-containing

thyroid hormone, thyroxine, by Kendall in December 1914, and its synthesis by Harington and Barger in 1927. Pioneer work on human endemic goitre carried out by McCarrison in India and by Marine and his colleagues in America has since been extended to almost every country in the world.

Studies of iodine metabolism and thyroid function in farm animals have inevitably lagged behind those relating to man, and interpretation of experimental findings must take account of variation between different species. It is established, however, that by virtue of its part in the structure of the thyroid hormones, iodine is one of the essential trace elements, and in view of the profound influence of the thyroid gland on all metabolic activity the physiological function of iodine is of considerable importance in livestock husbandry.

The literature on the physiology of iodine and its relation to endemic goitre and the treatment of thyroid dysfunction in man and animals exceeds in scope and quantity that of all the other trace elements combined (Underwood, 1956). It is therefore evident that in this review of iodine in relation to animal health and production, only a brief survey is possible of the most important aspects and their practical implications to the livestock owner.

A useful review of information existing up to 1927 was given by Orr and Leitch (1929) but until about 1930 analytical techniques were not sufficiently accurate to determine the small amounts of iodine present in many biological materials and thus provide reliable data upon which to base definite conclusions. The evolution of knowledge concerning thyroid function was described by Harington (1933). Recent advances have been founded upon increasing knowledge of the biosynthesis of thyroid hormone, the application of radioactive isotope techniques, and the discovery of substances which interfere with the utilization of iodine by the thyroid gland. As such substances are now known to occur naturally in many feeding-stuffs, particularly in *Brassica* crops, they are of special interest to those concerned with the nutrition of livestock.

NATURAL SOURCES OF IODINE

IODINE IN SOIL AND WATER

Soils are richer in iodine than the rocks from which they are derived, their content being dependent upon the balance of a number of enriching and depleting agencies. Atmospheric precipitation, the

natural decay of vegetation containing iodine and the adsorptive capacity of humus and clay serve to increase the iodine content of soils, whereas leaching and cropping are important depleting agencies.

According to Goldschmidt (1954), the factors which determine a regional iodine deficiency in soils are: distance from the sea, low annual atmospheric precipitation and recent glaciation, the last being perhaps the most important. Although this latter point is disputed by Beeson (1958), the frequency distribution of goitre in North America and in a number of countries in Europe, Asia and Australasia, shows a close correlation with the areas and extent of quaternary glaciation where soils have not yet been sufficiently saturated with post-glacial air-borne oceanic iodine.

Contrary to the popular conception, however, soils in the neighbourhood of the sea are not always richer in iodine than those inland since any influence on iodine content will also depend upon the direction of the prevailing wind, the amount of precipitation and the nature and reaction of the soil. In New Zealand, Shore and Andrew (1934) noted some sandy soils near the sea to be exceptionally low in iodine, and Fraps and Fudge (1939) found sandy soils near the Texas coast to be lower in iodine content than other soils of the state, possibly related to the greater rainfall in the coastal regions.

Iodine is fixed by the organic matter or by the fine fraction of heavier soils so that, generally speaking, heavy-textured clays and loams contain most iodine, and light sandy soils poor in colloidal matter contain the least. This relationship is shown in Table 27.1 derived from a compilation of world literature on the iodine content of soils.

TABLE 27.1. *Iodine content of soils*

Kind of soil	Number of Samples	Iodine content µg./kg. Range	Avg.
Clay	373	trace–68,740	7319
Clay loam	314	trace–58,120	5904
Loam	587	trace–70,000	3802
Sandy loam	493	trace–60,000	3574
Sand	202	trace–32,000	2113

(From Chilean Iodine Educational Bureau, 1956)

Peive (1959) notes that in the U S S R , in areas of sandy soil, light loam or sod-podzolic boggy soils which are deficient in cobalt and copper, a deficiency of iodine is also usually observed

No sharp distinction can be drawn between the iodine contents of different geological strata although a significant relationship has been established, largely due to other factors involved, between geological formation and the incidence of iodine deficiency as indicated by human thyroid enlargement (Murray *et al* , 1948)

The iodine content of drinking water has been widely used as an index of the iodine status of rocks and soils and has frequently been related to the incidence of human goitre Chatin, whose extensive investigations have been referred to, concluded that water from formations rich in lime and magnesium contains relatively little iodine and that rivers fed by glaciers are also low in iodine especially during the melting of the snow It should be noted, however, that the iodine content of water is not always a reliable indication of that of the soil from which it flows Soils of high colloidal content such as clay and peat, though themselves rich in iodine, may give up little to the water percolating through them, whereas from other soils of relatively low content the iodine may readily be dissolved

Murray *et al* (1948) have suggested that for human beings a 'non-goitrous' level for the iodine content of drinking water should be put at 5 µg per litre or more for hard waters, and possibly 3 µg per litre for soft waters There is, however, insufficient evidence to suggest whether this index might also be applied to farm livestock

IODINE IN PASTURE

Following the discovery of iodine in marine vegetation, in which the amounts are often comparatively large and simple to detect, and with the development of increasingly delicate methods of analysis, it was gradually established that iodine is contained in all plants It is not yet known whether this element is essential to plant as to animal life, though no species of plant has been grown in an iodine-free environment. Modern research places iodine in the class of 'beneficial elements' which although not found essential, may in trace quantities materially assist growth or metabolic efficiency (see Chilean Iodine Educational Bureau, 1959)

Although the soil is the primary source of iodine for both waters and crops, there may be little or no correlation between the iodine

content of a soil and that of pasture growing on it. This is shown (Table 27.2) by the data of Simpson (1930*a*) and Butler *et al.* (1956).

TABLE 27.2. *Relative iodine contents of soil and pasture* (μg. per kg. dry matter)

Soil	Pasture				Author
	Not specified	Perennial ryegrass	Short-rotation ryegrass	Cocksfoot	
176	—	1,350	230	225	Butler *et al.*
200	140	—	—	—	Simpson
300	—	1,600	168	258	Butler *et al.*
600	130	—	—	—	Simpson
700	110	—	—	—	Simpson
848	—	—	—	125	Butler *et al.*
853	—	1,500	150	175	Butler *et al.*
1,500	130	—	—	—	Simpson

Butler *et al.* showed a similar lack of correlation between the iodine content of soil and that of several varieties of clover.

Few data are available concerning the absorption of atmospheric iodine by pasture but experiments with other crops and recent work with radioactive isotopes suggest this may be of importance. Most values for the iodine content of pasture lie between 100 and 1,000 μg. iodine per kg. of dry matter but within this range the content may be influenced by a number of factors:

Locality and soil type. Geographical influence differs according to the region concerned and is largely dependent on soil characteristics. Thus hill pastures in New Zealand are often richer in iodine than valley pastures (Simpson, 1930*a*) whereas in the Carpathian regions mountain-grown fodder is reported as having a lower iodine content than that of the valleys (Zaderiĭ, 1956). As in the case of soils, and for similar reasons, proximity to the sea does not necessarily imply a higher iodine content of pasture although in favourable circumstances this may be so.

Fixation of iodine in humic and clay soils may restrict its uptake by plants, and the reaction of the soil appears to be of particular importance. According to Simpson (1930*a*) alkaline soils, although rich in iodine, may give up little to plants growing on them, whereas acid soils give up their iodine more readily. Beeson (1958) notes that in the United States iodine does not appear to be deficient in the humid

regions, where the soils are highly leached but acid in reaction, whereas in the north-west iodine deficiency is associated with alkaline soils although in a semi-arid climate with a minimum of leaching

There is, however, some evidence that the critical pH for maximum uptake of iodine by plants is not constant (Borst-Pauwels, 1959) and no precise conclusions can as yet be drawn

Season and stage of growth Seasonal variation in the iodine content of New Zealand pasture was reported by Hercus and Roberts (1927) who found highest values in June and July (winter), and by Simpson (1930*b*) who found maximum values in autumn and early winter and minimum values in summer, with lesser variation according to area and climatic conditions Previously, Orr and Leitch (1929) had noted that in serial analyses of samples of Scottish pasture from the same field, figures for August, September and October were 350, 470 and 580 μg iodine per kg dry matter respectively Blom (1934) recorded seasonal variation in the iodine content of several species of South African pasture grasses, and the limited data of Calderbank *et al* (1960), referred to below, suggest a marked fall in the iodine content of pasture associated with onset of growth in spring followed by a gradual return to initial values during late summer and autumn

Although there is thus some agreement that the iodine content of mixed grass sward increases during the growing season, reaching a maximum in late autumn, Butler *et al* (1956) have shown that this does not necessarily apply to individual grasses (see Table 27 3) Also it should be noted that this seasonal variation is largely or entirely a reflection of the stage of growth and is therefore subject to the secondary influences of cropping, rainfall and environmental temperature

Butler *et al* found a seasonal variation in the iodine content of clovers, Broad red, Montgomery red and subterranean varieties having maximum values in spring, while white clover had a consistently higher iodine content with maximum values during winter Wright and Sinclair (1958) found the iodine content of spring-sown kale in New Zealand to be 1,200 μg per kg dry weight in December–February (summer) declining to 600–700 μg per kg in July (winter) Kale, however, frequently has an iodine content appreciably lower than these values might suggest Jones (1960) refers to preliminary work suggesting that kales, particularly marrow-stem varieties, are poorer sources of iodine than mixed grass and clover swards

Botanical composition Bourcet recorded in 1899 a wide variation in iodine content between plant species and even between plants of the

same species, and Fischer (1931) found the iodine content and capacity for iodine absorption of individual species of vegetables to vary considerably. However, although Young *et al.* (1936) noted the different iodine contents of four pure strains of pasture grasses, no great attention was paid to this quality of pasture until the recent work of Butler and his colleagues in New Zealand. This has shown that variation between species and strains of grasses is the most important single factor determining the iodine status of New Zealand pastures (Butler and Johnson, 1957) and that the percentage iodine content of the herbage is a strongly inherited characteristic. Iyer (1958) has also noted that the outstanding feature of the iodine content of Indian fodder plants is the wide variation within the same species as well as between different species growing in the same locality and soil type.

Table 27.3 from the data of Butler *et al.* (1956) illustrates the influence of species and season on the iodine content of some common

TABLE 27.3. *Seasonal influence on the iodine content of pasture grasses*

Grass	Iodine content (µg. per kg. dry weight)			
	Spring	Summer	Autumn	Winter
Perennial ryegrass	1,300	1,300	1,350	1,860
Italian ryegrass	600	650	900	1,225
Short-rotation ryegrass	160	275	230	575
Cocksfoot	225	275	83	78
Yorkshire fog	55	83	60	78

(From data of Butler *et al.*, 1956)

pasture grasses growing on soil with a relatively low iodine content of 1,760 µg. per kg. dry weight.

The iodine content of various grasses grown (in containers) on a humic sandy soil from the Netherlands did not, however, show such wide variation (Borst-Pauwels, 1959):

	µg. iodine per kg. dry matter
Cocksfoot	305
English ryegrass	300
Timothy	225
Meadow fescue	220
Kentucky bluegrass	150

The high iodine content of the New Zealand strain of perennial rye-grass is particularly noteworthy

Beeson (1958) reports that in the northern and western United States, in contrast to the general situation in the area, there are many isolated sites where the iodine content of vegetation is very high Typically these sites are poorly drained with a high water table where sedges and rushes predominate

On the basis of the New Zealand work it would theoretically be possible, assuming no limitation is imposed by the availability of soil iodine, for the plant breeder to produce by selection strains of grasses having a high iodine content even where the soil content is relatively low It seems unlikely, however, that this would prove worth while in practice in view of the facility with which an adequate intake of iodine by livestock may be ensured by direct supplementation of their food or by appropriate fertilizer treatment of the pasture

Fertilization It has been shown repeatedly that the iodine content

TABLE 27 4 *Iodine content of English pastures*

Field	Fertilizer	Iodine content (µg /kg dry matter)						
		Before application	After application					
			May	June	July	Aug	Sept.	Oct
1958 1	Chilean nitrate	250*	1,140‡	490	330	1 040	350	600
2	Nitro chalk	280*	—	260	330	620	370	390
1960 3 (half)	Chilean nitrate	667†	195	—	270	282	—	500
	Nitro chalk		150	—	250	248	—	500
1960 4 (half)	Chilean nitrate	781†	145	—	330	363	—	673
	Nitro chalk		125	—	280	350	—	640

* May † March
‡ Possible residual contamination due to low rainfall

of crops can be increased by the application of iodine in various forms to the soil or nutritive medium. Recent experimental evidence suggests that iodate ions are absorbed less rapidly by grass than iodide ions but that the application of iodate has a more lasting effect (Borst-Pauwels, 1959).

Although specific iodine preparations are in use in some parts of the world, seaweed and guano are the most iodine-rich organic fertilizers, and Chilean nitrate of soda is the only inorganic fertilizer in common use containing a significant proportion of iodine (0·01–0·02 per cent).

A number of investigators have referred to the favourable influence of Chilean nitrate of soda on the iodine content of forage crops (see Chilean Iodine Education Bureau, 1950). Table 27.4 shows the iodine content of English pastures on the same farm, sampled at approximately monthly intervals throughout the grazing season, after application of a single dressing of Chilean nitrate of soda or 'Nitro-chalk' at the rate of 2 cwt. per acre (Calderbank *et al.*, 1960):

Data from five investigations in the Netherlands (Chilean Nitrate Agricultural Service, 1959) show in three instances a positive influence (> 10 per cent) on the iodine content of pasture of fertilization with Chilean nitrate compared with other nitrogenous fertilizers.

The relative importance of the various soil and botanical factors in relation to this variation in response are not yet known.

IODINE INTAKE BY GRAZING ANIMALS

The grazing animal may obtain iodine from the pasture itself, from drinking water and from the ingestion of soil which may contaminate water or pasture, the effective intake depending upon the quantity of each ingested, their content of iodine and its availability to the animal. Although it is not always easy to apportion the relative importance of these sources, it is evident that in most circumstances the water supply does not itself provide a major part of the iodine intake of farm animals, or of human beings. A cow drinking 10 gallons of water containing 7 µg. iodine per litre would receive 318 µg. iodine from that source—less than one-tenth of the daily intake of iodine from average pasture. Low iodine content of drinking water may, however, be related to the incidence of iodine deficiency where either the water provides a marginal fraction of the total iodine intake or where its low content reflects also deficiency in soil and pasture.

Little is known about the relative availability to the animal of iodine occurring in various forms or organic combination in pasture and in

foods of plant, or animal, origin The hardness of water has been shown to be an important factor influencing the incidence of human goitre and it is possible that this applies also to animals Excessive hardness may affect not only the utilization of iodine contained in the water, but also that of iodine ingested from other sources

Orr and Leitch (1929) calculated that the intake of iodine by cows grazing Scottish pasture of high iodine content would be about 30 mg per day and that sheep on grass would ingest from 0 4 to 2 0 mg iodine daily Russell (1944), however, notes that it is doubtful if the results of pasture analysis accurately reflect the iodine intake of the grazing animal since it is difficult to get samples free from soil and the animal may be able to utilize some of the soil iodine eaten with the pasture. Several authors have noted a high iodine content in salt and earth 'licks' sought after by stock and by wild animals (Kalkus, 1920, Waters, 1938) Although, therefore, the major source of iodine for grazing animals is the pasture itself, ingestion of soil may in some circumstances provide a significant contribution.

In view of the many factors affecting the utilization of iodine by animals the critical iodine content of pasture below which deficiency in grazing animals is likely to occur may vary according to situation and circumstance Thus, attempts to correlate the incidence of goitre in livestock with the iodine content of the pasture and hay eaten have not been entirely successful. Although the average iodine content of samples from goitre areas may be less than from healthy areas, values deemed adequate in some districts are sometimes lower than those considered goitre producing in others (Russell, 1944, Murray *et al*, 1948)

In New Zealand, Simpson (1930*a*) reported goitre in lambs associated with pasture containing 100–200 μg iodine per kg dry matter, and Butler and Johnson (1957) state that they have confirmed in four instances an association between goitre in lambs and pasture containing less than 300 μg iodine per kg of dry matter

Lehr (1960) has suggested that pasture iodine contents below 300 μg per kg dry matter should be regarded as deficient and contents of 300–600 μg per kg as marginal. For practical guidance this is probably the best interpretation of the information at present available

IODINE METABOLISM

Iodine is present both in plants and in foods of animal origin partly in inorganic form and partly in organic combination. Probably most

of the ingested iodine is reduced to iodide in the alimentary tract, and is thereafter rapidly absorbed. The rate of absorption suggests that in the ruminant considerable absorption of iodine, as iodide, takes place from the rumen (Garner and Sansom, 1959).

Absorption of iodide is practically complete and most of the iodine appearing in the faeces probably represents dietary iodine which has been absorbed and resecreted. Iodide is removed from the circulation mainly by the thyroid gland and the kidneys, the clearance ratio depending on the state of activity of the thyroid, and in the lactating animal a significant proportion of the circulating iodine is secreted in the milk.

Swanson *et al.* (1957) quote unpublished data of Monroe *et al.* who found the actual distribution of iodine^{131} in the thyroid gland, milk and excretions of a cow killed three days after dosing to be: thyroid 11·7 per cent, urine 43·7 per cent, faeces 17·6 per cent, milk 7·2 per cent.

Garner and Sansom (1959) has summarized the fate of I^{131}, administered orally to lactating cows, in a diagram (Fig. 27.1).

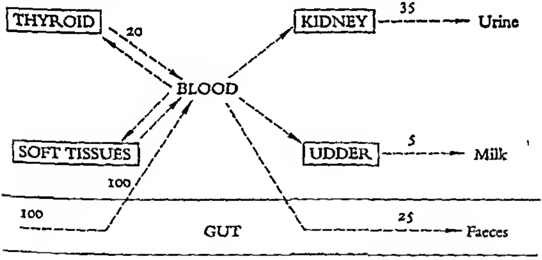

FIG. 27.1. I^{131} fate in lactating cows (from Garner and Sansom, 1959).

IODINE IN THE THYROID GLAND

All animal tissues contain iodine but of the total iodine in the body 20–40 per cent is concentrated in the thyroid gland. Iodine entering the gland is rapidly incorporated into colloid or thyroglobulin which is the initial substrate of the iodination process leading to the synthesis of thyroid hormones and is also the medium of storage of the hormones within the gland.

The iodine content of the thyroid varies principally with the activity of the gland and iodine intake in the diet, and to a lesser extent with age and individual Near the end of gestation foetal, thyroids, despite their smaller size, can take up as much iodine as the maternal gland Thus, the tracer iodine concentration in the thyroid of the bovine foetus is seven times higher than in that of the mother (Gorbman *et al*, 1952) and in sheep the foetal capacity increases until it is four times greater than the maternal at about the fourth month of gestation, and continues at this level until parturition (Wright and Sinclair, 1959)

Normal thyroids of mammals contain 0 2–0 5 per cent of iodine, dry weight, and variation between species seems to be small Marine and Lenhart (1909) showed that hyperplasia occurs when the iodine concentration falls below 0 1 per cent dry weight, equivalent to approximately 0 03 per cent fresh weight Mason (1933) in a survey of New Zealand sheep and lamb thyroids found increase in weight of the gland with fall in percentage iodine content to be negligible above 0 03 per cent fresh weight, and experimental evidence comes from data of Andrews *et al* (1948) given in Table 27 5

Table 27 5 *Effect of iodine on the lamb thyroid*

Treatment of parent ewes	No of lambs examined	Lambs thyroids: Iodine content (per cent dry wt)	Weight (gm)	Hyperplasia (%)
Not given supplementary iodine	147	0 021 only 3 glands above 0 1	5 71	65
Given supplementary iodine	86	0 404 only 3 glands below 0 2	0 829	1 16

(From Andrews *et al* 1948)

Wiertz considers the critical iodine content of calves' thyroids to be in the region of 0·04 per cent fresh weight, rather higher than the values quoted above. The same author discusses in some detail variation in thyroid weight and histological activity which, in general, increase with decreasing iodine concentration.

For an account of the biosynthesis of the thyroid hormones the reader is referred to the book of Pitt-Rivers and Tata (1959).

IODINE IN BLOOD

Iodine in the blood exists in two fractions, inorganic iodide and protein-bound iodine (PBI). The former remains relatively constant in different states of thyroid activity, but is greatly elevated with increased intake of iodine. Protein-bound iodine is, in contrast, sensitive to changes in thyroid activity and the level in serum is generally regarded as an index of the amount of circulating hormone. It may, however, also be influenced by increased iodine intake for variable, and in some cases considerable, lengths of time (Mason, 1932; Allcroft *et al.*, 1955; Long *et al.*, 1956). Ingestion of iodine in certain forms appears to have a particular effect on blood PBI—remarkably high levels in cattle reported by King and Lee (1959) were found to be related to provision of a mineral supplement containing iodine in the form of cuprous iodide and diiodosalicylic acid.

In view of the importance of blood PBI as an index of thyroid activity other possible sources of variation may be briefly considered:

Age. There is general agreement that PBI levels decrease with advancing age (Long *et al.*, 1951; Sorensen, 1958). Lewis and Ralston (1953*a*) recorded average plasma PBI levels of: calves under 24 hours 14·8 µg. per 100 ml., 24–48 hours 10·8 µg. per 100 ml. and 3 days–18 months 6·8–7·9 µg. per 100 ml. Calves at birth had 8·9 µg. PBI per 100 ml. which rose to 15·0 µg. per 100 ml. after the ingestion of colostrum.

The same authors (Lewis and Ralston, 1953*b*) suggested ranges of protein-bound iodine for normal cattle as follows:

	µg. per 100 ml.
Calves under 2 days	8·0–18·0
2 days–12 months	3·5–12·0
1–2 years	3·5–10·0
Cows over 2 years	3·0– 8·0

Further data, however, seem to be required before normal ranges can be regarded as firmly established (see table below)

Breed Breed variations in protein-bound iodine levels found by various workers are given in Table 27 6, but it may be noted that material and method were not in all cases strictly comparable.

TABLE 27 6 *Protein-bound iodine levels in blood of different breeds of cattle*

Breed	Authors			
	Reece and Man (1952)	Long *et al* (1952)	Allcroft *et al* (1954)	Sørensen (1958)
	µg iodine per 100 ml			
	serum	serum*	plasma	serum
Jersey	4 6 5 0	4 19		3 9 4 0
Guernsey		3 42	3 2 4 0	
Brown Swiss	3 7	3 24		
Ayrshire		2 95		
Friesian/Holstein		2 90	2 4-3 2	
Black & White Danish				3 8
Red Danish				3 7
Danish Shorthorn				3 2
Aberdeen Angus	4 2			
Beef breeds		2 19		

* Mean values corrected for age

Pregnancy Lewis (private comm to Underwood, 1956) has suggested that the rise in protein bound iodine level associated with human pregnancy does not occur in cattle but Sørensen (1958) and Kiesel and Burns (1960) found higher PBI concentrations in pregnant compared with non-pregnant cows of 39 per cent and 46 per cent respectively Annison and Lewis (1959) however, found no significant difference between plasma PBI values of pregnant ($3\frac{1}{2}$ months) and non pregnant sheep

Lactation A higher concentration of protein-bound iodine in blood taken from cows during the first half of lactation compared with that taken during the second half was reported by Sørensen (1958) which he considered reflects the normal trend in milk and butterfat secretion. Lennon and Mixner (1957) found PBI values for pregnant non-lactating cows and for lactating, non-pregnant cows of 3 78 µg

per 100 ml. and 4·96 µg. per 100 ml. respectively, suggesting the relatively greater effect of lactation in the animals used, for which the stages of lactation and pregnancy were not reported.

Environmental temperature. An inverse relationship between the environmental temperature and protein-bound iodine levels has been observed by Sørensen (1958), Hall *et al.* (1959) and others. Johnson *et al.* (1958) in a study of factors concerned in the comparative heat tolerance of Jersey, Holstein and Red Sindhi × Holstein cattle found serum PBI levels to parallel changes in heat production suggesting thyroid involvement in the process of adaptation.

As a reflection of the level of circulating thyroid hormone, protein-bound iodine values are usually depressed in conditions associated with hypothyroidism. Allcroft *et al.* (1954) found low PBI values of 0·8–1·6 µg. per 100 ml. and 1·6–3·2 µg. per 100 ml. in Friesians and Guernseys respectively, compared with 2·4–3·2 µg. per 100 ml. and 3·2–4·0 µg. per 100 ml. in controls, associated with a high incidence of aborted, stillborn and weakly calves, whilst Lewis and Ralston (1953*b*) found the average PBI level of 19 problem breeders to be 3·7 µg. per 100 ml.—significantly lower than that of their normal herd (4·84–4·97 µg. per 100 ml.).

In an area associated with human goitre, Ewy and Bobek (1959) found the mean serum PBI level of Polish Red cattle to be: calves up to 1 year 5·68 µg. per 100 ml., cows 3·0 µg. per 100 ml. In 4 out of 82 animals PBI values below 1·5 µg. per 100 ml. indicated hypothyroidism.

Robertson *et al.* (1958) found no significant effect on PBI level in cattle of a variety of stress (mainly disease) factors considered together, but point out that any effect might have been limited by the acute nature of the conditions investigated. It is interesting to note however that, of individual conditions, retention of the placenta was associated with a PBI value of 2·72 µg. per 100 ml. compared with an average value of 3·63 µg. for all conditions and 4.22 µg. for normal controls.

Reference to the diagnostic value of protein-bound iodine determination is made in a later section.

IODINE IN MILK

The iodine content of milk is highly variable depending principally on the level of dietary intake. The average iodine content of cow's milk is approximately 40 µg. per kg. and the content of goat's and ewe's milk appears to be similar or perhaps slightly higher (see Chilean

Iodine Educational Bureau, 1952). Literature on the subject (with the notable exception of Binnerts, 1956) has recently been reviewed by Archibald (1958).

The influence of dietary intake is illustrated in Table 27.7, showing the difference between mean iodine content of milk from two groups of cows on seven farms, one group on each farm receiving a special iodine supplement of 400 mg. potassium iodide per week in addition to

TABLE 27.7 *The effect of iodine feeding on milk iodine*

Month	Milk iodine (µg. per litre)	
	Group A	Group B
	Iodine supplement	Normal rations
February	235	51
March	128	74
April	177	87
	Spring grazing No supplement Reduced rations	
May	17	15

(From Bounds *et al.*, 1960)

normal (supplemented) commercial rations fed to both groups. On turning out to grass, the iodine supplement was discontinued and the other rations reduced.

The marked fall in iodine content of the milk in May is probably related in part to increased yields, but also suggests reflection of a low iodine content of spring pasture.

Regional variation in the iodine content of milk was considered by Shore and Andrew (1934) to depend on variation in the iodine content of the soil, but Binnerts (1956) found such an influence only in the case of marine clay with a particularly high iodine content.

Although milk from coastal areas tends to be somewhat higher in iodine content than that from inland districts (see Archibald, 1958) this is not always the case, as could be expected from the varying influence on soil and pasture iodine contents to which reference has already been made. Sjöstrom (1957) found the milk from four coastal

dairies in Sweden to contain an average of 13·8 µg. of iodine per litre compared with an average of 8·1 µg. per litte from 14 inland dairies, but in Holland Binnetts (1956) found distance from the sea to have no significant influence.

A considerable proportion of the iodine in milk is protein-bound although this apparently is not thyroxine, to which the mammary gland has been shown to be impervious (Reineke and Turner, 1944), and neither milk nor colostrum possesses the calorigenic properties associated with thyroid hormone. Lewis and Ralston (1953*a*) found the protein-bound iodine content of colostrum to be greater than that of milk, although varying from cow to cow.

Factors other than the level of dietary intake which have been considered to affect the iodine content of milk include the following.

Stage of lactation. According to Garner and Sansom (1959), results of experimental work do not indicate an effect on the secretion of I^{131} into the milk due to stage of lactation, except perhaps through its influence on milk yield.

There is, however, general agreement that colostrum is richer in iodine than milk produced later (see Chilean Iodine Educational Bureau, 1952). Binnerts (1956) found that the colostrum of the first two days was richer in iodine and that thereafter the iodine content of the milk was inversely correlated with yield. Equilibrium between iodine intake and output in milk was reached in about a week.

Season. Conflicting evidence of a seasonal effect on the elimination of I^{131} in milk has been presented by Lengemann *et al.* (1957) and Garner and Sansom (1959), and on the content of stable iodine in milk by Hanford *et al.* (1934) and Matthews *et al.* (1939). Shore and Andrew (1934) suggested that seasonal variation in milk iodine is due to seasonal variation in soil contamination of forage, but it is unlikely that this affords a general explanation. Binnerts (1956) found high winter values related partly to the decline in milk production and partly to differences in iodine supply.

It seems that any such effect is largely dependent on seasonal variation in intake of iodine and thyroid metabolism.

The iodine content of milk has been widely studied in relation to the incidence of human endemic goitre although correlation may be obscured particularly by supplementation of animal feeds. Thus, Hughes *et al.* (1959) found no significant difference in the iodine content of milk from farms in low and high iodine areas but found a

significant difference between winter and summer milk (20 µg compared with 60 µg per litre) related to difference in the consumption of concentrate rations containing iodine supplements However, a broad correlation between the iodine content of milk and the incidence of goitre is shown in Table 27 8 derived from published figures in the world literature

TABLE 27 8 *Percentage distribution of values for the iodine content of whole cows milk*

µg Iodine per litre	Goitre areas	Non-goitre areas	Not Specified	All areas together
0–20	52 94	6 25	11 54	22 03
21–40	47 06	43 75	50 00	47 46
41–60	0 00	37 50	26 92	22 03
61–80	0 00	6 25	3 84	3 40
above 80	0 00	6 25	7 70	5 08
	100 00	100 00	100 00	100 00

(From Chilean Iodine Educational Bureau 1952)

The above values agree closely with the average value of 43 µg per litre for the iodine content of cow's milk noted by Archibald (1958) although Bartlett *et al* (1949) quote data of the Central Veterinary Laboratory, Weybridge, indicating a normal value without supplementary dietary iodine of 15 µg per litre In cows suffering from iodine deficiency, giving birth to goitrous calves, Minakov (1952) found the milk to contain 24 µg iodine per litre when the animals were stalled and 30 µg per litre at pasture

The importance of milk iodine in human nutrition is worthy of note Milk has long been recognized as one of the principal sources of iodine in the human diet (Fellenberg, 1926) and Binnerts (1956) stresses the importance of cows' milk as a source of iodine particularly for expectant and nursing mothers and young children In municipalities in the Netherlands where iodized salt is used in bread-making the proportion of human iodine intake supplied by milk is only 5–10 per cent, but in other areas the proportion varies from 20 to 65 per cent of the total intake Similarly, in Sweden, milk products account for 30 per cent of the iodine supplied in human foods (Sjostrom, 1957)

There is reason to believe that in Britain also, milk is a major source

of iodine for the human population (Hughes *et al.*, 1959) in which the incidence of endemic goitre is still a matter for concern (see Kelly and Sneddon, 1960).

THYROID FUNCTION

The primary function of the thyroid gland is regulation of cellular oxidation and hence of the basal metabolic rate, and Barker (1951) suggests that the thyroid may be concerned exclusively with energy metabolism and yet indirectly be involved in making the necessary energy available for many specialized processes. Pitt-Rivers and Tata (1959), however, refer to a growing belief that the thyroid hormones have a specific action on growth processes independent of their function as metabolic regulators.

Whether or not there is any genuine separation of function, it is evident that the thyroid gland plays an important part not only in the regulation of general body metabolism, but also in survival of the new-born, in growth and development, reproduction, lactation and adaptability to environmental conditions (see Andrews, 1950). Thyroid activity also has a marked effect on water and mineral metabolism. Brochart *et al.* (1960) consider that the thyroid plays an important role in calcium and phosphorus metabolism in cattle, and reference is made elsewhere to a possible association with bovine hypomagnesaemia.

Thyroid activity is chiefly regulated by the anterior pituitary hormone thyrotrophin (see D'Angelo, 1954), and in the complicated interrelationships which exist between the thyroid gland, the adrenals, and the gonads, there is also evidence of mediation by the pituitary. Secretion of thyrotropbin stimulates thyroid activity in response to increased utilization of thyroid hormone. Increased thyroid output in turn depresses the pituitary secretion thus serving to maintain a functional balance in accord with body requirements. If, for some reason such as iodine deficiency, the full requirement for thyroid hormone cannot be met, increased secretion of thyrotrophin causes, in an attempt to provide more hormone, a compensatory enlargement of the thyroid gland known as goitre. This is discussed more fully elsewhere.

Until comparatively recently it was accepted that the circulating thyroid hormone is composed of thyroxine bound to protein, but following the identification of triiodothyronine in human plasma (Gross and Pitt-Rivers, 1952) and subsequently in the blood of various animals, the circulating hormone is now regarded as composed of

both thyroxine and triiodothyronine. A comprehensive account of the thyroid hormones and their physiological action is given by Pitt-Rivers and Tata (1959).

Andrews (1950) has pointed out that development of the various types and breeds of farm animals has involved unconscious selection for thyroid activity. An interesting illustration of this evolutionary process comes from an extensive study of the effect of thyroid deficiency upon bodily growth and skeletal maturation in sheep by Todd *et al.* (1938). They conclude that the result of consequent inhibition of velocity of growth without prolongation of the growth period is to reduce the proportions of the limbs to those of unimproved wild sheep.

With increasing knowledge of the economic importance of thyroid function in terms of animal production the possibility of artificial modification of thyroid activity has received considerable attention (see Blaxter, 1946). Varying degrees of hyperthyroidism may be produced by feeding iodinated protein or synthetic thyroxine and hypothyroidism can be induced by feeding anti-thyroid drugs, notably thiouracil and its related compounds. These latter substances are commonly known as goitrogens since with continued use, they may produce discernible thyroid enlargement or 'goitre'.

The terms 'thyroprotein' and 'iodinated protein', although not specific, are frequently applied to any iodinated protein preparations possessing thyroid activity, which they owe to their partial content of thyroxine. Synthetic thyroxine is now available which, being a pure substance, has obvious advantages in respect of standardization and dosage and is generally preferable to iodinated protein (Bailey *et al.*, 1949).

The effects of thyroprotein and antithyroid drugs on cattle, sheep and pigs, with particular reference to possible practical applications, have been reviewed by Blaxter *et al.* (1949), Blaxter (1952) and Winchester and Andrews (1953).

The natural occurrence of goitrogens is discussed later in relation to thyroid dysfunction.

Discussion of thyroid function here will be limited to aspects of particular interest in relation to animal production.

GROWTH

It has been established beyond doubt that the thyroid hormone is essential for growth during early life in man, monkeys, ruminants, rodents and birds (Pitt-Rivers and Tata, 1959).

The maturing skeleton is particularly sensitive to thyroid deficiency and depriving a young animal of thyroid hormone by surgery or by feeding diets low in iodine or high in goitrogenic agents greatly retards growth as a result, at least in part, of delayed osseous development (Underwood, 1956). Becks *et al.* (1950) have suggested that, in bone, pituitary growth hormone stimulates growth only, while the thyroid controls both growth and differentiation. Lascelles and Setchell (1959) noted that hypothyroidism in lambs, induced by feeding methylthiouracil to pregnant ewes, delayed maturation of the bone to a significantly greater degree than bone growth.

The possibility of using protein-bound iodine values, as an index of thyroid activity, to determine the potential performance of beef cattle and of pigs, has been suggested by Kunkel *et al.* (1953) and Gawienowski *et al.* (1955). Kunkel *et al.* compared serum PBI levels with the rate of live-weight gain in both individual animals and in groups of beef calves. Groups which showed a wide variation in protein-bound iodine exhibited wide variation in rate of gain, and in ten individually fed Herefords a high correlation between efficiency of gain and PBI levels was found.

Since protein-bound iodine levels vary with age, the period at which they are determined is of some importance. Gawienowski *et al.* (1955) related average daily gains and certain body measurements of pigs to serum PBI levels, but as these were determined at the time of slaughter (at 215 lb. weight), they do not necessarily reflect the levels in young animals upon which any predictions of performance could be based.

Singh *et al.* (1956) found higher thyroid activity in ewes related to faster weight gains in twin lambs probably due largely to increased milk consumption (see below); ewe lambs with higher thyroid activity gained faster than those with lower thyroid activity.

Although existing data are insufficient to support definite conclusions it seems there is an optimum level of thyroid activity for both growth and efficiency of food conversion, deviation from which is associated with lower rates of gain.

Retardation in growth has frequently been associated with hypothyroidism due to iodine deficiency or some other antithyroid factor. In human infants the extreme type of dwarfism known as cretinism was at one time common in goitrous regions. In such areas administration of iodine during adolescence increases the rate of growth as well as reducing the size and incidence of goitre (Stocks, 1927).

Jovanović *et al* (1953) recorded weakness, inco-ordination and stunted growth in various domestic animals associated with goitre, and Evvard (1928) noted that potassium iodide fed to pigs in a mildly iodine-deficient area resulted in greater growth and in feed economy even though no observable signs of goitre were apparent

In some cases administration of goitrogens has produced significant increases in efficiency of food conversion by pigs without markedly decreasing rates of gain, but administration for more than six weeks has usually depressed growth rates The feeding of goitrogens to weaners has given unfavourable results (Winchester and Andrews, 1953)

For the most part results of goitrogen administration have been inconsistent in all species possibly because the optimum conditions of age, dosage and duration of administration have not yet been established

In view of the changing rate of thyroid function with advancing age, Winchester and Andrews (1953) have suggested that a thyroprotein-goitrogen sequence might result in more efficient gains than those obtained with either material used alone Much more research is needed, however, before any major practical possibilities can emerge

Besides total body weight the growth of certain tissues, notably the skin and its covering, is also markedly retarded in hypothyroidism. Poor growth of wool or hair and poor condition of the skin are characteristic symptoms of iodine deficiency Administration of iodine has been reported to have a beneficial effect in delayed shedding of hair among young cattle in a tropical climate (Matson, 1931) Wool production, because of its special importance, is considered separately in a later section

MILK YIELD

Stimulation of lactation in a cow by the administration of thyroid hormone was first reported in 1896 by Hertoghe whose observations remained almost unnoticed until Graham (1934) described the effect again in greater detail Subsequently it was established that thyroid activity is an important factor in regulation of the rate of milk secretion (see Folley, 1956), and a great deal of attention has been paid to the possibility of artificially influencing milk production by administration of thyroxine or iodinated protein. The effect of thyroxine administration is greatest during mid-lactation (Herman *et al*, 1938) but the response is highly variable even under identical environmental con-

ditions. With continued administration there is a diminution in response and most of the evidence suggests that long-term stimulation does not result in substantial increases in production (see Blaxter, 1952).

Bartlett and Hutton (1959) who investigated the effect on lactating cows of subcutaneous implantation of thyroxine tablets found that a dose of 280 mg., judged to be comparable with a daily oral dose of about 70 mg., appeared to give satisfactory stimulation without undue ill effects. They confirmed, however, that the milk stimulating effect is reduced or rendered negative after a period of about 12 weeks by a decline in the natural secretion of the recipient's thyroid gland. A similar response was noted by Leech and Bailey (1953) who reported an extensive investigation of the effect of treatment with thyroxine and iodinated casein on the health of lactating cows in which they found a slightly increased incidence of digestive and metabolic disorders and a slightly decreased incidence of mastitis.

It may be concluded that the value of thyroxine or iodinated protein to stimulate milk yields in cattle is limited and use should be selective. Advantages are likely to be restricted to individual cases and circumstances; in general any overall increase in production, and profit, is likely to be small (see Blaxter, 1946, 1952).

In sheep and pigs stimulation of milk yield by this means has been used to indirect advantage in increasing the growth rate of their offspring. Hart (1957) has shown a lactopoietic effect in ewes implanted with thyroxine after lambing and Labban (1957) found that feeding thyroxine to the lactating ewe increased milk production and increased the weight at weaning of the lamb by about 5 lb. Similarly, the use of thyroprotein to increase milk production of lactating sows in order to accelerate the rate of growth and weight at weaning of the young pigs has also been reported (Johnson *et al.*, 1959), although negative results were obtained by Dudley *et al.* (1959).

A similar effect due to natural variation in thyroid secretion rate has been demonstrated by Singh *et al.* (1956) who found that Shropshire ewes with high thyroid activity tended to produce faster-gaining twin lambs than ewes with low thyroid activity. No relationship was apparent in the case of single lambs, suggesting that although ewes with low thyroid activity may produce enough milk for a single lamb, this may be a limiting factor in the successful rearing of twins.

Pipes (1956) found a significant correlation between thyroid activity of dairy cows and peak milk production during subsequent lactation, and the possibility of predicting the milking performance of cattle by

determination of their thyroid secretion rates has been discussed by Sørensen (1958).

Lowered milk production is a frequent symptom of clinical iodine deficiency in lactating animals (Shand, 1952; Jovanović *et al*, 1953) Suleimanova (1956) found that production of both milk and fat were improved when cows in an iodine-deficient region received supplementary potassium iodide during the grazing season.

MILK QUALITY

Graham (1934) showed that the increased milk yield of cows following administration of thyroid hormone is accompanied by an increased yield of milk fat. This finding was confirmed by Folley and White (1936) and by other workers, using both thyroxine and iodinated protein (see Blaxter *et al*, 1949), but there is considerable disagreement regarding the extent and duration of the increase. In some cases the increase in fat content is proportionately higher than that of yield, thus increasing the fat percentage to a significant extent (Reineke, 1942, Van Landingham *et al*, 1944). Low doses of thyroid hormone in particular, may increase the fat content without increasing milk yield (Smith and Dastur, 1940, Reece, 1944) and there is some indication that cows with low-fat milk show the greatest response.

There is relatively little change in other milk constituents (see Blaxter, 1952) although Folley and White (1936) and others have demonstrated an increase in solids-not-fat largely due to increase in the lactose content

Bartlett *et al.* (1949) found, in eight experiments with grazing cows, an average increase of 0 10 per cent fat, and in five experiments on indoor rations an average increase of 0 46 per cent. The SNF percentage showed slight increases in ten out of thirteen experiments, the average increase being 0 04 per cent Blaxter (1952) has suggested that the exaggerated response in fat content when the cows were on controlled indoor rations may have been related to a state of physiological undernutrition which is known to increase the fat content of milk

It could be expected to follow from the above observations that in the contrasting state of thyroid hypofunction due to iodine deficiency a deterioration in quality of the milk would occur, particularly as regards its fat content, which could be corrected by the administration of iodine Several early workers, in fact, observed the effects of feeding extra iodine to lactating cows and reported the yield of fat to

increase, the percentage being unchanged or slightly raised, and in some instances recorded also an increase in solids-not-fat (see Maurer and Ducrue, 1928). Since administration of iodine would not, in itself, be expected to stimulate milk secretion, it seems probable that these results were due to correction of subclinical iodine deficiency. Improved milking performance may itself contribute to iodine deficiency due to increased loss of iodine in the milk (Hausmann, 1937; Minakov, 1952).

Wendt (1929), who reported the favourable effects of feeding an iodized mineral mixture (compared with a non-iodized mixture) to dairy cows over a period of three years, emphasized the necessity, if full benefits are to be obtained, to feed the iodized mixture through at least one dry period and one lactation. Minakov (1952) observed an increase in the fat content of milk following the administration of potassium iodide to cows to control goitre in their calves. In support of these observations Sørensen (1958) in a detailed study found the thyroid secretion rate and the iodine requirement of lactating cows to be closely correlated with butterfat production and it is noteworthy that the level of circulating protein-bound iodine is higher in Channel Island than in other breeds of cattle. Sørensen's findings, however, were not confirmed by Lennon and Mixner (1958). Obviously, not every case of low-fat milk can be attributed to thyroid dysfunction or iodine deficiency, but it is apparent that provision of adequate dietary iodine may eliminate one possible cause, at very low cost. At the same time, not the least effect of iodine feeding on the quality of milk is the increase in content of iodine itself to which reference has already been made.

WOOL PRODUCTION

Thyroid activity has repeatedly been shown to have an important effect on wool production. Maqsood (1950) found that mild hyperthyroidism resulted in an increase, while hypothyroidism resulted in a decrease in fibre length but the diameter was not affected; and Ferguson *et al.* (1956) noted a marked thyroid effect on the development of the wool-producing follicles, particularly the secondary follicles, their normal development requiring thyroid hormone in excess of that needed for body growth in general. Labban (1957) has suggested that in view of the high iodine content of hair, even when this is produced at a reduced rate, iodine may be an essential component of hair and that thyroxine may thus not only increase follicle metabolism but also act

as a source of iodine It seems unlikely, however, that iodine for structural purposes need necessarily be provided through the complex agency of a hormone

Hart (1957) found that in Romney sheep treated with thyroxine implants there was a definite improvement in wool grade amounting to as much as half a commercial grade interval He has suggested, however, that there may be breed differences in the response of wool growth to thyroxine in regard to both weight increase and grade improvement No such improvement was noted in similar observations on Corriedale sheep by Coop and Clark (1958) Ferguson (1958) found that thyroxine treatment caused an increase in feed intake necessary to maintain body weight and the net efficiency of wool growth declined Myers and Ross (1959) have emphasized the possibility that the observed effect of thyroxine on wool growth may, at least in some instances, be due to its correction of a subclinical iodine deficiency or to its action in overcoming some other goitrogenic factor. In two trials comparing the effects of thyroxine and iodine administration on Romney ewes they found no significant effect on fleece weight or grade

Hart has suggested that in many fat-lamb producing areas of New Zealand the use of thyroxine as a means of removing surplus weight prior to tupping may be justified on this score alone, any improvement in wool growth or grade being a welcome additional return Coop and Clark (1958) point out, however, that when feed is scarce or in only moderate supply and especially when the standard of pasture control and efficiency of pasture utilization is already high, thyroxine is not likely to increase overall efficiency The carrying of additional stock is more likely to increase the efficiency of pasture conversion except in the case of the over-fat ewe or where there is a temporary feed surplus

Although there is thus some doubt about the effect of thyroxine in increasing wool production there is no doubt about the deleterious effects of iodine deficiency Numerous authors refer to the scanty wool seen in iodine deficiency and Hopkirk and Dayus (1930) observed that iodine-deficient lambs may have coarse hair instead of the normal lambs' wool. Lowered wool production in enzootic iodine deficiency was noted by Jovanovic *et al* (1953). It is apparent from the work of Ferguson *et al* (1956), referred to above, that deficiency in the growing lamb may permanently reduce the quality of the adult fleece due to incomplete development of the secondary wool follicles

REPRODUCTION

Underwood (1956) has pointed out that reproductive failure is often the outstanding symptom of iodine deficiency and consequent impairment of thyroid function in farm animals. It is therefore interesting that complete thyroidectomy is not incompatible with the production of apparently normal offspring, the probable explanation being that, in the presence of a sufficient supply of iodine, foetal thyroid function may be adequate to maintain pregnancy.

There is, in fact, some evidence that the thyroid of the foetus may contribute to the requirements of a thyroid-deficient mother. Spielman *et al.* (1945) found in a heifer thyroidectomized on the 46th day of her first pregnancy, that growth was static for a period of about 20 weeks but was resumed during the last ten weeks of gestation. After parturition no further growth took place until the latter part of the subsequent gestation when it was again resumed. A similar observation on a thyroidectomized goat was reported by Reineke and Turner (1941)

a reciprocal balance between the hormones of the pituitary, the ovary and the thyroid Imbalance in this hormonal mechanism will not necessarily result in complete reproductive failure, but usually leads to great irregularity Meites (1953) has suggested that thyroid dysfunction may both reduce the secretion of gonadotrophic hormones by the pituitary and alter the gonadal response, but the precise interrelationships involved remain to be elucidated It seems that the principal influence of thyroid activity on reproduction is in relation to mammalian intra-uterine development The effect on ovulation is relatively less both in mammals and in birds

Abortion and stillbirth have long been recognized in association with iodine deficiency although in other cases the gestation period of goitrous young may be prolonged, probably depending largely on the stage of pregnancy influenced (Allcroft *et al*, 1954)

Jovanovic *et al* (1953) in their investigation of enzootic goitre in various domestic species noted decreased libido in males, suppression of signs of oestrus and a high percentage of sterility Iodine-deficient sows farrowed small litters with evidence of progressive mortality of other embryos having occurred during the course of gestation Stewart (1959) has also reported that there is increasing evidence that disturbances of the dietary intake of iodine and other minerals can affect the fertility level in cattle and Suleimanova (1956) found that reproduction in cows in an iodine-deficient region improved when they received supplementary iodine during the grazing season

THYROID DYSFUNCTION

The physiological state associated with normal thyroid function is termed euthyroidism, and aberrations from this state related to inadequate or excessive thyroid secretion are known as hypo- and hyperthyroidism respectively In man, disordered function and structure of the thyroid are encountered more often than abnormal activity of any other endocrine gland (Astwood, 1954), and Andrews (1950) has suggested that deviations from normal thyroid function are probably more common in domestic animals than is generally believed Both hypo- and hyperthyroidism may be associated with thyroid enlargement or goitre, but whereas both conditions occur widely in man, hyperthyroidism appears to be comparatively rare in animals

GOITRE

The term 'goitre' includes all conditions of the thyroid gland associated with an increase in its size but most commonly refers to enlargement associated with the functional disturbances of hypo- and hyperthyroidism referred to above. Toxic goitre, related to hyperthyroidism, is so called because of its association with the 'toxic' features of increased heart rate, tremor and hyperexcitability; and thyroid enlargement due to this condition, to thyroiditis, or to thyroid cancer will not be considered here. 'Simple', non-toxic, goitre has been defined as 'any enlargement of the thyroid gland which is neither inflammatory nor malignant and not associated with toxic features'. The genesis of simple goitre is essentially a process of cellular hypertrophy and hyperplasia, in an attempt to overcome an insufficiency of hormone or to secure an adequate intake of iodine in the face of a diminishing supply. When the hormone–iodine balance is restored, the gland usually reverts to a state of normal activity although there may be some per-

endemic goitre areas and by the unequivocal demonstration that administration of iodine prevents goitre (Trotter 1959) It is now generally accepted that the level of dietary iodine is of paramount importance for the proper working of the thyroid gland (Pitt-Rivers and Tata, 1959)

Simple deficiency of iodine may occur when the available supply is inadequate for normal requirements or it may become apparent only when the requirement is increased by the demands of high-level production, especially lactation and intensive breeding

Elmer (1938), dealing with the human, pointed out that loss of iodine in milk can result in depletion of the mother s iodine reserve inducing a negative iodine balance which should be compensated by an increased iodine intake It is to be expected that this consideration might apply with even greater force in the case of the dairy cow and experience in several countries has suggested this to be the case Reference is made elsewhere to the increased incidence of goitre in calves in Finland with the development of intensive dairy farming and, in Austria, Hausmann (1937) noted that goitre in calves did not occur under primitive conditions of feeding but only on farms where concentrates were used and high milk yields aimed at

Minakov (1952) observed the occurrence of goitre in calves at an experimental farm where between 1937 and 1941, the annual milk yield per cow was increased from a little over 5 000 lb to nearly 9 000 lb When the higher yields were reached goitre appeared in the calves suggesting the iodine intake to be insufficient for the development of the foetus and the simultaneous production of a high milk yield During the war a scarcity of concentrates led to lowered yields —and no goitre After the war when high yields were again achieved the goitre reappeared Minakov noted that with increase in milk yield the iodine requirement increased more than the requirement of other organic and inorganic constituents

Certain goitrogenic substances, which are discussed below, may be considered to induce iodine deficiency in so far that they prevent the uptake of iodine by the thyroid gland and that their effect may be overcome by increasing the level of iodine in the diet

Trotter (1959) considers that iodine deficiency however produced, is probably the major cause of human sporadic (as well as endemic) goitre Certainly an overwhelming proportion of thyroid dysfunction in farm livestock may be overcome by suitable augmentation of their dietary iodine intake

Goitrogens. Reference has been made earlier to the use of antithyroid drugs for the artificial suppression of thyroid function. Consideration is given here to naturally occurring goitrogens which are of practical significance to the livestock owner. The recognition of goitrogens in foodstuffs stems from the discovery by Chesney *et al.* (1928) that rabbits fed exclusively on cabbage developed goitre, which was followed by the demonstration of goitrogenic properties in various foodstuffs, notably in members of the *Brassica* genus (see Greer, 1950). Hercus and Purves (1936) reported an extensive outbreak of goitre in lambs from ewes which had for some months been fed exclusively on turnip roots. Young rabbits sent from the laboratory to the farm to be fed on the same turnips developed greatly enlarged thyroid glands within 60 days. Dayus (1937) also refers to outbreaks of goitre in New Zealand in which some factor in addition to iodine deficiency was suspected, believed to be associated with the feeding of swedes, rape and turnip tops.

In 1949 Astwood and his colleagues reported the isolation of an antithyroid factor from the edible root of rutabaga (swede) and white turnip, and from the seeds of turnip, cabbage, kale and rape. The identity of this substance was confirmed by synthesis as L-5-vinyl-2-thiooxazolidone. It was not then detected in some other *Brassica* seeds nor in the edible portions of cabbage, kale, cauliflower or broccoli (Astwood *et al.*, 1949), but its identification in cabbage, kale and other species has since been reported (Virtanen *et al.*, 1958; Altamura *et al.*, 1959). Vinylthiooxazolidone exists in plants in a combined form from which it is liberated by enzyme action; the goitrogenic activity is destroyed by cooking due to inactivation of the enzyme.

With increasing knowledge and experience two types of goitrogen have been recognized:

Wright and Sinclair (1958) considered kale to contain a goitrogen of the thiouracil type from the pattern of uptake of iodine[131] by the thyroid and its discharge by thiocyanate, which view has been substantiated by the work of Virtanen *et al* (1958) referred to above. This however, does not explain the experimental and clinical finding that the goitrogenic effect of kale is prevented by iodine feeding (Shand, 1952, Sinclair and Andrews, 1954) Although there is some indication that iodate affords partial protection against the goitrogenic effect of thiouracil in sheep (Wright, 1959), it seems probable that kale contains goitrogens of both types, the iodine-responsive fraction being of predominant clinical significance The most important goitrogenic factor in kale is, in fact, probably thiocyanate which this and other members of the *Brassica* genus have been shown to contain in appreciable concentration (Michajlovskij and Langer, 1958)

Clements and Wishart (1956) consider that a significant amount of goitre in Tasmanian children is due to a goitrogen in the milk of cows feeding on chou-moellier (marrow-stem) kale and on some cruciferous weeds Calves of cows fed chou-moellier also developed marked thyroid hyperplasia Wright (1958) has suggested that the children appear to have been already suffering from inhibition of iodine binding and that the milk contained a goitrogen of the thiocyanate type—inhibiting thyroid uptake of iodine and discharging unbound iodine already accumulated—possibly derived from iso-thiocyanates in the forage plants Clements (1957) considers that epizootic goitre in lambs in south Tasmania during 1956 was also probably associated with the ingestion of cruciferous weeds

Care (1954) showed that linseed is goitrogenic for sheep, the goitrogen being thiocyanate produced by detoxication of cyanide liberated in the rumen and Flux *et al* (1956) have demonstrated a goitrogenic effect of white clover also related to its cyanogenetic glucoside content. Cunningham (1955) notes that goitre in lambs does occur when the ewes have been fed pasture containing clovers, but whether this is a result of iodine deficiency or of antithyroid substances or of both is not determined He suggests that increases of the cyanogenetic glucoside content may in some years be a precipitating cause of goitre in an environment where iodine intake is borderline Vandersall *et al* (1958) have noted that a reduction in milk production observed with abrupt change to grass-legume silage cannot always be attributed to lower digestible nutrients and as a result of determination of depressed iodine[131] uptake they have postulated that a goitrogen may be formed

during fermentation of the silage. Affleck (1958) has recorded an outbreak of goitre in foals fed heavily on irrigated lucerne.

Other dietary factors which have been associated with the occurrence of goitre include the levels of calcium and phosphorus intake, although the mechanism of goitrogenesis is not clear. Svanberg (1951) refers to goitre in certain districts of Sweden which appears generally to accompany 'licking disease' and disappears where superphosphate is systematically applied.

Hignett (1959) (referring to work of Allcroft, Hignett and Scarnell) reported the experimental production of goitre in calves by feeding their dams during pregnancy on rations in which the phosphorus (P_2O_5) content exceeded that of calcium (CaO). The results are shown in Table 27.9.

TABLE 27.9. *The effect of calcium and phosphorus on experimental production of goitre in calves*

Ration	Cow No.	Calf thyroids Weight gm.	Calf thyroids Group average
$CaO > P_2O_5$	5	16·9	10·8
	11	10·6	
	3	8·0	
	9	7·8	
$P_2O_5 > CaO$	2	31·6	21·9
	8	29·8	
	4	15·5	
	6	10·4	

(From Hignett, 1959)

The wide distribution of goitrogenic agents in nature (see Greer, 1950) and the fact that goitrogens may be produced in the course of normal metabolism, as in the detoxication of cyanide, have prompted the suggestion that animals may be regarded as being continuously subjected to varying degrees of goitrogenic interference (Salter, 1950), although when *Brassica* crops are being fed the effect of endogenously produced thiocyanate is likely to be overshadowed by that ingested in the food (Langer and Michajlovskij, 1958).

OCCURRENCE AND DISTRIBUTION

Goitre in animals has been reported from many countries throughout the world and iodine deficiency is considered by Allman and

Hamilton (1948) to be the most widespread in occurrence of any mineral nutritional trouble in grazing animals. The incidence of animal goitre roughly parallels in intensity the prevalence of human endemic goitre, reviewed by Kelly and Sneddon (1960). Trotter (1959), however, points out that as goitre occurs in every country of the world in which it has been looked for, the difference between endemic and non-endemic areas is only relative, and in farm livestock the manifestation of deficiency frequently depends upon the level of production and hence of iodine requirement.

The similar distribution of animal and human goitre has been noted by Hojer (1931), Jovanovic *et al.* (1953), Wiertz (1957) and others. Wiertz found goitre in newborn calves in the Netherlands to parallel both the distribution of goitre in man and of low iodine content in cow's milk.

Goats and Channel Island cattle seem to be particularly susceptible to iodine deficiency, possibly related to a higher normal level of thyroid activity. It is interesting that in countries as far apart as New Zealand, Yugoslavia and England, thoroughbreds have been considered more prone to goitre than other horses.

Sporadic goitre due to goitrogenic substances in the diet may obviously occur without geographical distinction and is most frequently associated with the use of *Brassica* crops for winter feeding. In practice, the effect of goitrogens may only become apparent in circumstances of borderline environmental iodine deficiency. Intensification of iodine deficiency by a goitrogen is well illustrated by experience in New Zealand where an outbreak of goitre in lambs from ewes grazed on thousand-headed kale was associated with 76 per cent mortality compared with 16 per cent mortality in lambs from ewes on mildly iodine-deficient pasture (Sinclair and Andrews, 1954). The effect of a goitrogenic diet is likely to be marked if fed during the period when the foetal gland is developing its high power of iodine concentration, which in sheep is during the fourth and fifth months of gestation (Wright and Sinclair, 1959).

A tendency to greater prevalence of iodine deficiency in very wet seasons, noted by Hignett (1952) and Affleck (1958), may be due to a number of factors, singly or in combination, including excessive leaching, lower iodine content of lush pasture and increase in the forage content of some goitrogen. Certain historical variations in the incidence of goitre, and the occurrence of iodine deficiency in animals grazing cultivated land allowed to revert or lie fallow referred to by

Affleck (1958), may be explained, at least in part, by ecological succession of goitrogen-containing weeds (see Clements, 1960).

Development of clinical hypothyroidism when for some reason hormone synthesis is inadequate, will obviously depend not only upon the intensity of demand for hormone but also on the extent of initial thyroid reserves. Hence a well-stocked gland may be able to withstand iodine deficiency or the influence of some other goitrogenic factor for an appreciable length of time. Hopkirk and Dayus (1930) reported over 100 lambs born dead with enlarged thyroids from 1,000 ewes which had been on iodine-deficient alluvial flats for two years, but not from 300 ewes which had been on the flats for only one year. Likewise, Southcott (1945) recorded the birth of dead or dying goitrous lambs to 40 per cent of two-toothed ewes when full and broken-mouthed ewes had a lambing percentage over 100 per cent with only two observed goitres, suggesting a cumulative deficiency accentuated by the higher metabolic requirements of the young ewes. A similar experience with breeding sows has been noted by Andrews (1950). As the farrowing season progressed there were significant increases in weight and epithelium height and a significant decrease in the iodine content of the piglets' thyroids suggesting gradual depletion of the sows' stored iodine.

It is obviously desirable that the level of dietary intake of iodine should at all times be sufficient to maintain adequate thyroid reserves. As the symptoms of both simple and induced iodine deficiency are identical, they will be considered together in the following discussion without aetiological distinction.

SYMPTOMS

The classical symptoms of iodine deficiency in farm animals were described by Welch (1917), Kalkus (1920) and Evvard (1928) and an account has recently been given by Jovanović *et al.* (1953). They fall into four main categories: thyroid enlargement (goitre); poor condition of the skin and its covering; reproductive disturbances; and lowered production and vitality. As iodine has no known physiological function other than as part of the thyroid hormones, all these symptoms are presumably related to a disturbance of thyroid metabolism. The factors which determine that certain symptoms should be most prominent in particular cases are, however, not fully understood and must be associated with metabolic variations between species and within species at different times and in different circumstances.

Thyroid enlargement In domestic mammals, hair, wool and folds of loose skin and tissue obscure the thyroid region, and external appearance is not a reliable indication of thyroid enlargement. It is most often seen in affected lambs and calves, less often in foals and is not usually externally visible in pigs As long ago as 1928 Evvard drew attention to the unfortunate emphasis laid on goitre and hairlessness as sole and distinctive symptoms of iodine deficiency leading to incorrect diagnosis when these gross manifestations are not evident

Jovanovic *et al* (1953) in an examination of 2 000 cattle found clinical goitre in about 5 per cent compared with 20 per cent of cases at post-mortem examination, and in goitrous lambs described by Shand (1952) increase in thyroid size was not noticeable to the eye although it could be felt on palpation and was perfectly obvious at autopsy Similar findings have been reported by Hignett (1953), Allcroft *et al* (1954) and others Wright and Sinclair (1958), studying the goitrogenic effect of thousand-headed kale, have shown that although ewes producing goitrous lambs may show no clinical goitre they still suffer considerable interference with their thyroid function

In normal animals thyroid weight is related to total body weight, approximate average values for thyroids of newborn lambs and calves are 1 gm. and 10 gm respectively but there is an appreciable range of normal variation.

Since thyroid enlargement is related to proliferation of its cellular elements it follows that histological changes will take place before any macroscopic enlargement is apparent Wiertz (1957), who compared results of estimations of thyroid weight, histological activity and iodine content from a series of 627 newborn calves considered none of these criteria alone to be ideal. He places them in order of significance and time of development histology, iodine content, weight.

Condition of the integument Poor growth and condition of the skin and its covering are among the most constant features of iodine deficiency This influence of thyroid dysfunction may be regarded as a reflection in a particular tissue of its profound effect on growth and maturation of the body as a whole. Setchell *et al* (1960) noted however, in observations of neonatal mortality in lambs associated with goitre, that although affected animals generally had a coarser coat than usual, many showed apparently normal coat development. In extreme instances particularly when iodine deficiency is operative during intra-uterine development, hair growth ceases entirely and the young are born naked with smooth, glistening unpigmented skins

Thus calves and pigs born to iodine-deficient mothers are often hairless with thick, pulpy skins, but hairlessness does not seem to be a conspicuous feature in foals. Less severe deficiencies involve corresponding degrees of disordered condition of the pelt—rough, dry, wrinkled skins with a harsh, staring coat, scanty wool or hairiness of the fleece. Analogous changes may be seen in the hooves which are thin-walled, brittle and underdeveloped.

Reproductive disturbances. Reproductive failure is often the outstanding symptom of iodine deficiency in farm animals, and stillbirth in particular has been recognized as a symptom since the condition was first described (see Kalkus, 1920; Evvard, 1928). Actually, foetal development may be arrested at any stage, leading to early death and resorption, abortion, stillbirth, or the live birth of weak and sometimes moribund young. When the young are born alive, pregnancy is frequently prolonged. The varying pattern presumably depends upon the degree of deficiency and the stage of pregnancy influenced. In Finland, von Wendt (1929) noted an increase in abortion and sterility in cattle and goitre in calves associated with the development of intensive farming.

More recently, Hignett (1953) has described a clinical syndrome in cattle apparently associated with thyroid dysfunction in which there is abortion or extended gestation, prolonged parturition with the birth of dead or weak calves, retention of foetal membranes and a high incidence of genital infection. In support of these observations Allcroft *et al.* (1954) found a high herd incidence of aborted, stillborn and weakly calves to be associated with hypothyroidism as evidenced by low plasma protein-bound iodine values and histological changes in foetal thyroids. Retention of the placenta as a feature of iodine deficiency in cows has also been noted by Moberg (1959) who observed retained placentae to be 47 per cent fewer in a group of 252 herds given supplementary iodine than in a group of 127 herds which served as controls.

As well as disturbances during pregnancy and at parturition, infertility in cattle as a consequence of iodine deficiency has been recognized by Hignett (1952), Jovanović *et al.* (1953), Dawson (1958) and others. Hignett has reported that irregular return to oestrus is common with anoestrus in some cases, and Jovanović *et al.*, who found a high percentage of sterility in cows in a region of enzootic goitre, noted suppression of the signs of oestrus to be a characteristic feature. Experimental work showing that deficiency of thyroid hormone

causes aberration of the oestrus cycle (see Reincke and Soliman, 1953), and failure to exhibit the physical manifestations of oestrus (Spielman *et al*, 1945) has thus been borne out by clinical observation in the field

The thyroid gland also plays an equally important part in the maintenance of male fertility (see Maqsood, 1952) Thyroid deficiency is characterized in particular by a decline in libido and deterioration of semen quality Hignett (1952) has noted these features as symptoms of iodine deficiency in bulls, and Jovanović *et al* (1953) observed decreased libido in stallions affected by goitre

Lowered vitality and production Physical and mental sluggishness is characteristic of hypothyroidism in all animals and lowered vitality is a frequent accompaniment of iodine deficiency in the newborn. Litters of iodine-deficient pigs frequently include a number of stillbirths with others dying soon after birth, goitrous foals and calves are often weak, and inability to stand and suck intensifies their initial debility

Shand (1952) has described the clinical pattern of iodine deficiency in ewes and lambs associated with intensive kale feeding of ewes during pregnancy The ewes gave little indication of thyroid dysfunction until near lambing time when they became rather fat and less energetic with poor udder development and a very poor milk supply The lambs were small, looked 'badly done' and carried little flesh with their skin thrown into folds They showed great lack of vitality and behaved stupidly with little idea about feeding or sense of direction A similar picture has been described by Setchell *et al* (1960) Mild cases may recover completely with suitable care and attention, but in other instances early weakness and underdevelopment may persist into adult life. Several authors have suggested that affected animals have an increased susceptibility to infection

Numerous authors call attention to features of iodine deficiency in adult animals which may seriously reduce productive efficiency In horses, working ability is diminished, in cattle and sheep, udder development is poor and milk yield reduced, in sheep, wool production is lessened and lowered in quality, and in parturient animals obstetric assistance may be necessary due to oversize of the foetus, or to failure of the uterus to contract and expel the young normally (see Kalkus, 1920, Welch, 1928, Shand, 1952, Hignett, 1952, Jovanovic *et al*, 1953, and others)

Thyroid dysfunction has also been suggested as a possible factor contributing to a number of metabolic disorders, notably bovine

ketosis and hypomagnesaemia (grass tetany). Robertson *et al.* (1957) found that ketotic cows had significantly higher levels of plasma corticosteriods and blood acetone, and significantly lower levels of plasma protein-bound iodine and blood sugar than control cows. They suggest that ketosis in dairy cattle may involve a relative adrenal-cortical insufficiency induced by hypothyroidism. Allcroft (1947) considered that an observed increase in the serum magnesium of cattle during a period of cabbage feeding may have been related to a goitrogenic effect. Conversely, Swan and Jamieson (1956) and Meyer and Schmidt (1958) noted a depression of blood magnesium under the influence of thyroprotein or thyroxine administration and the latter authors have suggested that the association of tetany with periods of low atmospheric temperature may be related to an increase in thyroid activity (see also Wilson, 1960). Tacken (1956) reported tetany in three of six cows which had not received iodine feeding during the winter and in the only one of 15 pregnant cows on the same farm which had received no iodine. The previous year, when no iodine was administered, tetany occurred 12 times in 16 animals. It seems that when serum magnesium levels are low, disturbance of thyroid activity may be an important factor in the onset of tetany.

Further research is necessary to elucidate the role of iodine deficiency in relation to these and other disorders.

DIAGNOSIS

Although symptoms described above may be obvious and even dramatic, the reader will recognize that not all of them are specific to iodine deficiency. Diagnosis may therefore be far from easy, especially when no thyroid enlargement is apparent. Some assistance may be derived from a knowledge of areas where natural sources of iodine are known to be relatively poor, or of the feeding of large quantities of crops known to be potentially goitrogenic. In these circumstances the precipitation of iodine deficiency is often related to increased production. Obviously, however, iodine may even then be only one of several deficient nutrients and in practice such features as poor condition, lowered production and impaired fertility may frequently be the common signs of multiple deficiency.

Thyroid enlargement and hairlessness of the newborn are more distinctive symptoms of iodine deficiency and when these occur diagnosis may be made with some confidence. Lascelles and Setchell (1959) have suggested also the diagnostic value in young animals of

changes in skeletal maturity Mention has already been made that goitre may be caused by specific antithyroid substances in the food as well as by simple iodine deficiency Since, however, in the majority of such instances the condition responds to iodine supplementation of the diet, these may be considered for practical purposes as cases of 'relative' iodine deficiency It has been stressed that external appearance is not a reliable indication of thyroid enlargement, particularly in adult animals When post-mortem material is available histological evidence of cellular hypertrophy may be observed before any gross enlargement of the thyroid is apparent

Determination of the percentage iodine content of the thyroid is of considerable value in supporting a diagnosis of iodine deficiency based on gross and histological examination A direct assessment of the avidity of the thyroid gland for iodine as an indication of sufficiency or deficiency, can be made by measuring the uptake of radioactive iodine isotopes, but unfortunately this procedure is hardly practicable except under laboratory conditions

A reasonably good index of thyroid activity is, however, provided by determination of protein-bound iodine in blood which, within limits, reflects the level of circulating hormone Although therefore this represents one of the few critical tests which may be applied to the living animal, interpretation must be guarded A low plasma PBI level will usually indicate hypothyroidism and probably iodine deficiency, but a normal or high level may be misleading It is always desirable therefore also to take into consideration other criteria of thyroid activity Johnston *et al* (1959) found PBI determination a questionable index of thyroid function and, of the various measures applied, thyroxine secretion rate was most closely related to metabolic rate Sørensen (1958) also found little correlation between PBI and thyroid secretion, but considered, nevertheless, that in general PBI is a better indicator of thyroid activity than limited experimental findings might suggest

It has been suggested that determination of the serum level of butanol-extractable iodine as a test of thyroid function has advantages over that of total PBI in that it measures only the thyroxine-like compounds of the serum and is not altered by the administration of iodides (see Man and Bondy, 1957) Data on this subject, however, are, as yet, inadequate for any firm conclusion to be drawn (see, for instance, Reece and Man, 1952)

It is also important to recognize that even with a low level of iodine

intake the thyroid gland, as a result of hypertrophy and over-activity, may succeed in restoring and maintaining a more or less normal rate of hormone output, and hence PBI level. This is achieved, however, only at the expense of endocrine and metabolic stress with consequent risk of imbalance and breakdown.

Summarizing, a diagnosis of hypothyroidism probably due to iodine deficiency, natural or induced, may be reached by consideration of history and circumstance; clinical symptoms; plasma protein-bound iodine level; and histology and iodine content of the thyroid gland itself. Finally, diagnosis may be reinforced by trial feeding of an iodine preparation, usually potassium iodide, at an appropriate level. Although in normal circumstances the toxicity of iodine is very low, a word of caution is necessary. When the thyroid gland is already enlarged and highly active the sudden administration of iodine may lead to a temporary overproduction of hormone with undesirable effects. Treatment should therefore always commence with small doses which may be gradually increased, and should be carried out under veterinary supervision.

CONTROL OF IODINE DEFICIENCY

Iodine deficiency can be controlled, simply and effectively, by providing supplementary iodine in the diet. Indeed, Cunningham (1955) comments that the ready response of animal goitre to iodine therapy has probably limited the study of goitrogens in the food of domestic animals, since the immediate economic question is solved when iodine is fed. In ensuring an adequate intake of iodine to support the health and productivity of farm livestock, it is necessary to consider both estimates of actual physiological requirements and the provision of reasonable practical allowances within the limitations of toxicity and economy.

IODINE REQUIREMENTS

The iodine requirements of grazing animals under varying conditions of management are not known with any degree of exactitude. This is both a reflection of the technical difficulties involved in their determination and recognition of the fact that results obtained under one set of conditions would be of limited practical value since they would vary according to the type of animal, class of production, environment and the nature of the diet. Also, experimental methods tend to

indicate minimum requirements below which certain detectable changes take place. In practice these may bear little relation to the optimum requirements of high-producing animals subject to the stresses inherent in any system of practical management.

Cattle. The iodine requirement of a dairy cow has been cited as being about 1 mg. per day or 50–100 μg. per 100 lb. body weight. This figure is derived largely from the calculations of Mitchell and McClure (1937) who applied the minimum iodine requirement of rats, determined experimentally by Levine *et al.* (1933), to the estimated heat production of a dairy cow giving 40 lb. of milk daily, and from Griem *et al.* (1942) who calculated the requirement of a 1,000-lb. cow from data relating to the iodine requirement of humans.

Apart from species considerations, Butler *et al.* (1956) emphasize that no account is then taken of goitrogens in the feed, nor is account taken of the loss of iodine in milk to which reference has been made earlier.

Sørensen (1958) found the iodine requirement of lactating cows, calculated from their thyroid secretion rate, to be closely related to butterfat production. According to Sorensen the iodine requirements of cattle are:

	mg. iodine per day
Calves	0·3–0·8
Bullocks	1·0–1·2
Non-pregnant heifers	1·2–2·3
Pregnant heifers (excluding foetal requirements)	1·3–4·6
Lactating cows	1 mg. iodine per 2·5 kg. (5·5 lb.) of milk of 4 per cent butterfat

In iodine balance experiments, Simon (1954) found the retention of iodine by four 1–1½-year-old cattle to vary from 329 to 888 μg. iodine per day on winter fodder and 539–1,036 μg. per day on summer grass.

Sheep. The iodine requirements of sheep, not subject to such excessive demands as the dairy cow, may be correspondingly nearer to the theoretical minimum requirements (50–100 μg. per day) calculated by Mitchell and McClure (1937), but the frequency with which sheep are fed on goitrogenic *Brassica* crops and the trend to increased lambing percentages and improved milking performance must raise the require-

ment, at least of breeding ewes, very considerably. Sinclair and Andrews (1958), referring to the prevention of goitre in newborn lambs from kale-fed ewes, found that two doses of 360 mg. potassium iodate, one given at about the beginning of the fourth month of pregnancy (when ewes were transferred to the *Brassica* crop), and the other at the beginning of the fifth month of pregnancy, effectively prevented mild to moderate goitre and greatly reduced the symptoms of severe goitre and prevented heavy neonatal mortality.

Myers and Ross (1959) found 10 mg. iodine given at fortnightly intervals, after an injection of 100 mg. to overcome any initial deficiency, adequate for sheep during a trial period of one year during which they were run on ordinary pasture with extra feeding in the form of hay, mangolds and turnips in late winter.

Pigs. The minimum iodine requirement of pigs was calculated by Mitchell and McClure (1937), as outlined above, to be 0·08–0·16 mg. iodine per day and Beeson *et al.* (1953) suggest there is evidence that the requirement for pregnant sows is approximately 0·2 mg. iodine per 100 lb. body weight and that it is somewhat less for growing pigs. In iodine balance experiments, however, Schneidemann (1952) found the daily retention of a growing pig to average about 1 mg. iodine and Sørensen and Moustgaard (1957) calculated the iodine requirement of 5-month-old Landrace pigs from their thyroid secretion rate to be 0·93 mg. iodine per day.

TOXICITY

It is possible to induce toxic effects by the administration of excessive quantities of iodine and iodides as with many other food substances, and, in therapeutic dosage, prolonged use of iodine preparations may lead to iodism, in which case it usually suffices to discontinue treatment for a few days (Garner, 1957). At nutritional levels, however, the margin of safety is very wide (Orr *et al.*, 1929; Green, 1938). Forbes *et al.* (1932) found that individual cows varied in their ability to tolerate iodine from 0·65 gm. to 2·13 gm. per day. Thirty milligrammes per 100 gm. live weight was excessive for calves, but with few exceptions 10 mg. per 100 lb. live weight was tolerated. Lambs given 33 mg. supplementary iodine daily showed no unfavourable effect, but they would not tolerate the same total quantity given in two doses per week. Thomson (1934) reported favourable effects of feeding 90 mg. iodine per head per day in the form of potassium iodide to a herd of dairy cows throughout five complete lactations.

Malan *et al* (1935) found that doses of 2 mg, 20 mg and 60 mg potassium iodide given daily to Merino ewes for a period of 30 months had no effect on their weights, wool production or reproduction and considered that ill effects ascribed to iodide feeding in earlier work were related to a concomitant deficiency of vitamin A In a further experiment (Malan *et al*, 1936) reproduction was abnormal in ewes receiving a potassium iodide supplement of 50 mg daily for twelve months and especially so with a diet low in carotene, but no other adverse effects were noted This work suggests that the safety margin in respect of iodine administration to sheep is approximately 50 times the nutritional requirement and the available data indicate that a similar or wider ratio applies also to other classes of livestock.

It may be concluded that with levels of iodine recommended for nutritional purposes the danger of toxicity to normal animals does not arise

PRACTICAL CONSIDERATIONS

It has been suggested that prophylaxis in respect of iodine deficiency is unnecessary in the absence of clinical manifestations or except in certain well defined regions From the above discussion, however, it is clear that the appearance of clinical symptoms represents an advanced state of thyroid dysfunction which may be preceded by appreciable economic loss Also, the use of large quantities of goitrogenic feeding stuffs may induce a relative deficiency in areas where the natural sources of iodine are in other circumstances, entirely adequate Shand (1952) has pointed out that shepherds have long known of the danger of feeding to pregnant ewes too much of certain crops, many of which are now known to contain antithyroid substances

It may be accepted therefore that a risk of iodine deficiency exists

(1) In iodine-deficient areas widespread throughout the world
(2) In marginal areas where intake is adequate to support natural existence but not to support enhanced levels of production
(3) When the food consumed contains appreciable quantities of goitrogens

The effect of goitrogens is obviously most marked when superimposed upon high level production or in marginal areas and it seems that the natural supply of iodine is rarely adequate to offset a combination of these factors

The possibility of ensuring an adequate iodine intake for grazing

animals by the use of iodine-containing fertilizers merits consideration. The available evidence suggests that natural iodine-containing fertilizers, notably Chilean nitrate of soda and seaweed, can make a useful contribution in this respect. In practice, however, supplementary iodine is most commonly given to animals in the form of mineral licks or pellets, or in powdered supplements incorporated in the concentrate feed. Use of an injectable iodized oil preparation has been reported by Myers and Ross (1959).

Iodine is usually added to foodstuffs in the form of potassium iodide although other compounds, particularly potassium iodate, have been shown to be satisfactory (Wright and Andrews, 1955). When potassium iodide is used, considerable losses of iodine can occur, especially in a warm or damp environment, by volatilization, leaching or interaction with other substances unless the iodide is suitably stabilized (Kelly, 1953). The iodates are, however, intrinsically stable and they have been adopted as a source of iodine by several countries undertaking the iodization of salt for human consumption. The use of iodates in animal feeding, in preference to iodides, is to be recommended particularly for the manufacture of salt licks which may be exposed for long periods to unfavourable weather conditions (Davidson *et al.*, 1951; Holman and McCartney, 1960).

In the United States the National Research Council committees on animal nutrition have noted that the use of iodized salt containing 0·015 per cent of iodine incorporated at a 1 per cent level of the grain ration has proved effective in preventing goitre and that when the iodized salt is stabilized to retard loss of iodine a product containing 0·01 per cent potassium iodide will probably provide the needed iodine supplementation (Loosli *et al.*, 1956).

This level of supplementation is calculated to supply, in the case of the dairy cow, 3½ times the theoretical minimum requirement (see above), but it is unlikely that this meets the optimum requirement of high-producing dairy cows or the requirements of animals consuming quantities of goitrogenic feeding-stuffs. In Britain the recommendation most generally adopted is one part of iodine in 2,000 parts of salt, or 0·05 per cent (Cuthbertson, 1954).

Several writers have drawn attention to the existence of borderline iodine deficiency in countries in which some degree of prophylaxis has already been adopted. Thus, in New Zealand, where it has been suggested that the amount of iodine permitted in mineral mixtures may be inadequate (Hickey, 1955), Myers and Ross (1959) have referred to

the occurrence of thyroid enlargement indicating the continued existence of sub-optimum intakes of iodine

Peltola and Vartiainen (1954) noted that thyroid enlargement in cattle in Finland has not been prevented by prolonged use of mineral supplements providing about 1 5 mg iodine per head per day Minakov (1952), on the other hand, found that administration to cows of 1 ml of a 1 per cent solution (10 mg) of potassium iodide per day successfully controlled goitre in their calves and was associated with an increase in the fat content of their milk.

Further study is required to evaluate the economic significance of borderline iodine deficiency, the remarkable affinity for iodine of the thyroid gland and its sensitivity to deficiency are highly suggestive

In view of the low cost of providing the small quantities of iodine required for dietary supplementation there is no reason why the risk of thyroid stress due to iodine deficiency cannot be almost entirely avoided.

Although available information on the varying iodine requirements of farm livestock is far from adequate, tentative suggestions may be advanced for practical guidance (Table 27 10)

TABLE 27 10 *Iodine requirements of farm livestock*

Class of livestock	Probable daily requirement (mg iodine)	Suggested daily allowance (mg iodine)
Dairy cows in milk	2–20*	3–30*
Other cattle	1–5	2–10
Breeding ewes	1–2	2 5
Other sheep	0 5–1	1–2
Breeding sows	1 2	2–5
Other pigs	0 5–1	1–2

* According to milk yield

The suggested allowances will provide a reasonable margin to meet normal contingencies and adverse factors but might be inadequate in exceptional circumstances as, for instance, when goitrogenic foods comprise a high proportion of the total diet of pregnant animals

In theory the desirable level of iodine supplementation, particularly for dairy cattle, will obviously vary widely between individual animals in a herd For practical purposes, when concentrates are fed in pro-

portion to milk yield, a general recommendation of $\frac{1}{4}$–$\frac{1}{2}$ an ounce of potassium iodide, or equivalent, per ton of concentrate feed (5–10 p p m iodine) would appear to be fully adequate The higher level should be employed when feeding only few concentrates and large quantities of *Brassica* crops

In the case of pigs receiving a substantial proportion of fishmeal in their ration this can usually be considered to provide a significant contribution to their iodine intake and the above allowances may then be halved

When stock are at pasture, particularly pregnant or high-yielding animals in iodine-deficient areas, and when grazing *Brassica* crops, free access to adequately iodized licks or pellets is advisable In British practice, levels of 250–500 p p m iodine have been found generally satisfactory

Thyroid dysfunction in farm animals may thus largely be prevented by ensuring an adequate intake of iodine in their diet measured in terms of a fraction of an ounce per ton of food ingested

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CHAPTER TWENTY-EIGHT

Plant Toxicology and Photosensitivity

R. J. GARNER

Introduction—Pasture plants: oestrogens and cyanogenetic glucosides, disease conditions—Common weeds of pasture: bracken and horsetails, buttercups, umbels, ragwort—Trees and shrubs, Forage crops—Roots—Photosensitivity.

In veterinary toxicology, particularly in recent years following the introduction of commercial agricultural preparations which are potentially extremely dangerous to stock, there has been a tendency to relegate poisoning by plants to a position of minor importance; there is, for example, no mention of them in McGirr's review (1956) of present-day toxicity problems. Although published statistics indicate that material from cases of plant poisoning constitutes 2 per cent or less of the total number of specimens submitted for toxicological analysis and subsequently confirmed (see, for example, Orr, 1952), there is equally no lack of evidence to demonstrate that severe losses are suffered annually from this cause. Further there can be little doubt that plant poisoning occurs much more frequently than is generally supposed but, since in most cases only small quantities of toxic material are ingested at any one time, the symptoms do not proceed beyond the stage of dullness, general malaise and inappetence and are not recognized for what they reflect.

What are the hazards presented by plant species to grazing stock? It comes as a surprise to the layman to learn that it is not unknown for some of the grasses and legumes which constitute the greater part of permanent pasture, at certain stages of growth, under certain climatic conditions or on certain soils, to cause serious disorders in livestock.

Many of the various forage and root crops used to supplement grazing if improperly prepared or stored or for other reasons not at all understood, may similarly become dangerous to animals consuming them. Other and more obvious hazards are presented by the common weeds of pasture, by hedgerow plants, by trees, bushes and shrubs growing either in the same field or on adjoining premises in a situation accessible to stock, and by no means least, by the careless and irresponsible disposal of garden rubbish and the trimmings from ornamental shrubs

Weeds, shrubs and the like are especially attractive to animals in the spring, after a winter off pasture At such a time, as Klussendorf (1956) says, 'anything green looks good, whether or not previous experience proves it so' Later in the year, when the grass has seeded and there is a scarcity of young green herbage, grazing stock may again turn to other sources of lush green food, but it is by no means always a shortage of wholesome greenstuff which drives them to eat noxious plants Forsyth (1954) cites many examples of animals developing a perverted taste for highly poisonous and even unpalatable weeds

Cattle are most frequently affected by plant and fodder poisoning Bohosiewicz (1955) states that the plants most commonly causing poisoning in this species are yew, water hemlock, spotted hemlock and autumn crocus in descending order of frequency This author also reports that, in Poland cases of plant poisoning in horses are mainly due to buttercups and, in sheep, to Cruciferae

The number of plants which can be considered to be potentially dangerous to grazing animals (with or without evidence to support the contention) is very large and a detailed account of the toxicology of individual species is beyond the province of this chapter It is therefore intended to discuss only the most important and the most interesting of the more common of the plant species known to be responsible for poisoning in livestock. Their toxicology is most conveniently dealt with under the following headings pasture plants common weeds of pasture, trees and shrubs, forage crops and roots A further section has been added on Photosensitivity This syndrome characterized by sensitivity to light, is best considered separately since it is common to poisoning from many widely differing plant species

For a more detailed account of the plants believed to be poisonous in the British Isles and in other parts of the world the reader is referred to the following authorities among others

British Isles: Long (1924), Wright (1943), Edwards (1949), Forsyth (1954).
South Africa: Steyn (1934), Van der Walt (1944*b* and other papers).
Australia: Hurst (1942), Bull (1953), Queensland (1953, etc.), St. George-Grambauer (1957), Gardner (1958).
New Zealand: Connor (1951).
India: Chopra, Bodhwar and Ghosh (1955).
U.S.A.: West and Emmel (1950), Sperry, Dollahite, Morrow and Hoffman (1955), Klussendorf (1956), Kingsbury (1958).

PASTURE PLANTS

The species to be considered under this heading belong mainly to the families *Gramineae* (grasses) and *Leguminosae* (legumes). Heather (*Calluna vulgaris* and *Erica* spp.) may make up a large part of heath and mountain pastures and these may also include a few (and harmless) members of the family *Juncaceae* (rushes).

OESTROGENS IN PASTURE PLANTS

It has become apparent that many plants contain substances having oestrogenic activity (Bradbury and White, 1954; Koller, 1955). The most important from the practical point of view is undoubtedly subterranean clover. It has been shown that the Dwalganup strain of this plant (*Trifolium subterraneum* L. var. Dwalganup) is responsible for serious losses to the sheep-breeding industry in Western Australia (Bennetts, 1944; Bennetts, Underwood and Shier, 1946). The oestrogenic compound has been identified as genistein (4, 5, 7-trihydroxyisoflavone) (Biggers and Curnow, 1954). The concentration of genistein is highest during the period of growth (when it may be as high as the equivalent of 0·01 mg. of oestradiol per 100 g. of dry matter) and is low in clover and hay. A derivative of genistein, the 4-methyl ether, known as 'biochanin A' has been obtained from short-rotation ryegrass (*Secale cereale* L. var. Rosen), perennial ryegrass (*Lolium perenne*) and red clover (*Trifolium pratense*) (Pope, Elwate, Simpson and Andrews, 1953; Bradbury and White, 1954).

Other oestrogenic compounds than the isoflavone group have been isolated. The chloroplast material from subterranean clover contains a phenolic oestrogen distinct from genistein (Australia, 1955). Another compound, apparently a coumarin derivative, has been isolated from

Ladino clover (*T repens* var, *ladino*), strawberry clover (*T fragiferum*) and lucerne (*Medicago sativa*) (Bickoff *et al*, 1957)

The low but definite oestrogen content of the early spring growth of the ryegrass quickly disappears and no oestrogen could be detected by Cunningham and Hogan (1954) in the later spring or autumn growth Oestrogenic activity is not destroyed by ensilage, lucerne silage has been said to be more oestrogenic than fresh lucerne (Pieterse and Andrews 1956)

A high concentration of oestrogen in spring grass in Britain was reported by Bartlett *et al* (1948) who considered that it might account for the known galactopoietic effects of the spring growth Rowlands (1957) has suggested that the intermittent occurrence of short periods of herd infertility reported in cattle in this country might be attributed to sudden changes in the amounts of oestrogen ingested Schoop and Klette (1952) have encountered in Germany a large-scale herd sterility in cattle which they ascribe to the high oestrogen content of the pasture (of the order of 2 gm per kg of dry matter) Oestrogenic material present in birdsfoot trefoil (*Lotus corniculatus*) and Ladino clover (*T repens* var *ladino*) may be responsible for delayed conception in ewes grazed on these species (Engle Bell and Davis, 1957)

Watson and Murnane (1958) believe that oestrogens in ryegrass and subterranean clover may be implicated in the aetiology of 'sheath rot'

In sheep pastured on subterranean clover the major problems encountered have been dystokia, prolapse of the uterus and persistent infertility The latter is associated with cystic changes in the endometrium which, as shown by Underwood and Shier (1951), if sufficiently severe, can persist indefinitely but there is no apparent disturbance in the oestrous cycle (Underwood and Shier, 1952) Underwood Shier and Peterson (1953) have further shown that the condition can be reproduced by continued intramuscular injection of stilboestrol in oil, dose levels as low as 0 11 mg of stilboestrol daily resulting in almost complete infertility The sterility in cattle described by Schoop and Klette (1952) was associated in many cases with a sterile metritis The udders of both pregnant and non-pregnant animals showed signs of swelling and in lactating animals there was a drop in milk yield, a rise in the cell content of the milk and inappetence

CYANOGENETIC GLYCOSIDES IN PASTURE PLANTS

Many grasses and legumes contain cyanogenetic glycosides—organic compounds containing a sugar and capable of yielding hydrocyanic

acid on hydrolysis. Quisumbine (1947) lists 25 species of the Gramineae including *Sorghum vulgare* (millet), *S. sudanense* (Sudan grass) and *S. halepense* (Johnson grass), *Cynodon plectostachyum* (giant star grass), *Holcus lanatus* (Yorkshire fog) and *Poa aquatica* and 52 members of the Leguminosae. The most important of the latter is white clover (*Trifolium repens*), certain strains of which contain the glycoside, lotaustralin, from which cyanide is liberated under the action of the enzyme, linamarase. White clover has been responsible for poisoning in cattle, particularly in New Zealand. The occurrence and significance of cyanogenetic compounds in plants have been discussed by Van der Walt (1944*a*) and Moran (1954). Cyanide poisoning from this source is of the greatest practical importance in South Africa and occurs with some frequency in the United States.

Cyanogenetic glycosides *per se* are not poisonous; it is the hydrocyanic acid which is liberated from them which is the toxic principle. This compound is normally released by the action of the specific enzymes which are set free when the plant tissue is damaged or begins to decay, but hydrolysis can occur within the intestinal tract of animals in the absence of the enzyme as a result of bacterial action within the rumen (Coop and Blackley, 1949).

The amount of free hydrocyanic acid within any particular plant varies with the stage of growth, the soil, climate, etc. (Van der Walt, 1944*a*). In Sorghum species hydrocyanic acid disappears from the stalks during the first three or four weeks of the life of the plant, but persists in the leaves until maturity (Willaman and West, 1916). The application of nitrate fertilizers favours a high hydrocyanic acid content (Pickney, 1924; Couch, 1932). A possible explanation of this has been provided by Worden (1940) who suggests that cyanogenetic glycosides are normal intermediates in the conversion of nitrates into plant protein. Climatic conditions, such as drought, which retard normal growth or lead to wilting bring about the liberation of large amounts of hydrocyanic acid in certain species (Steyn, 1934). It follows that the hydrocyanic acid content of cyanogenetic plants is extremely variable and that plants which are normally regarded as safe and are used for grazing, under conditions favourable to development of the maximum hydrocyanic acid content, can lead to fatal poisoning in animals consuming them.

Ruminants are particularly susceptible to poisoning from cyanogenetic plants since, as mentioned above, liberation of cyanide can take place as a result of hydrolysis by micro-organisms present in the

rumen Coop and Blackley (1949) found that peak production, concentration and absorption of hydrocyanic acid takes place within 10–20 minutes of sheep eating cyanogenetic plant material under suitable conditions Pigs and horses are less susceptible, possibly also because the gastric hydrochloric acid of simple-stomached animals destroys the specific plant enzymes (Dykstra, 1952)

Factors determining the toxicity of ingested cyanogenetic material to ruminants include, according to Van der Walt (1944*a*), the quantity of the plant ingested, the previous diet of the animal, the pH of the stomach contents, the percentage of total hydrocyanic acid present in the free state of the plant, the concentration of cyanide-liberating enzyme present in the plant, and the total hydrocyanic acid content of the plant Detoxification of cyanide by conversion into thiocyanate occurs very rapidly, so that should the rate of liberation of the poison from the ingesta be sufficiently slow no untoward effects would be expected In practice, therefore, it is only those animals that eat rapidly which are likely to suffer dire consequences The M L D of free lotaustralin (the glycoside of white clover) for sheep is said by Coop and Blackley (1950) to be 4 5±0 5 mg per kg body weight, and an intake of plant material equivalent to 4 mg per kg body weight of hydrocyanic acid can be regarded as definitely lethal if consumed fairly quickly

OTHER CONDITIONS ASSOCIATED WITH RAPIDLY GROWING PASTURE PLANTS

Bloat The grazing of lush young grass, green clover and particularly lucerne is frequently attended by 'bloating' in cattle The feeding of such forage crops as kale and rape has also been associated with bloat, especially when animals have been folded upon them. Most outbreaks in grazing animals occur on pastures containing a large proportion of clover, when the plants are in the immediate preflowering stage and have shown a phase of sudden growth The mechanism of the condition is apparently simple the gases which are produced during the process of microbial digestion of food within the rumen are not eliminated, accumulate and distend the organ with sometimes fatal results

The view that bloat is due to excessive gas produced primarily in greedy feeders has been discredited by the observation of Hancock (1954) that animals which bloat do not necessarily eat more, or eat more rapidly, than those which remain unaffected.

A great deal of attention has been paid to the possible presence in herbage causing bloat of toxic substances which might interfere with eructation and the activity of rumen muscle. Evans and Evans (1949) and Ferguson, Ashworth and Terry (1949; 1950) attributed the bloating properties of white clover and alfalfa, respectively, to the presence of hydrogen cyanide and a flavanoid, tricin. Heath and Park (1953) detected a cholinesterase inhibitor in white clover. However, favour now seems to be given to the view that the condition is due to the presence of substances (saponins and plant proteins and their hydrolysis products) which reduce the surface tension of the rumen liquor and hence tend to promote foaming. Gutierrez, Davis and Lindahl (1958), for example, have shown that alfalfa saponins are utilized by certain rumen bacteria, with resultant production of acids, gas and large amounts of slime. The latter forms stable foam in which the gases are entrapped in the ingesta as small bubbles and are prevented from escaping. Anti-foaming agents, particularly the recently introduced silicones, have been used successfully for both relieving and preventing the disease (Quin, Austin and Ratcliffe, 1949). Preliminary experiments have been carried out on the efficacy of emulsified peanut oil sprayed on to bloat-promoting pastures (Reid, 1958).

Hypomagnesaemia. There is ample evidence to show that conditions which stimulate rapid growth, for example, heavy dressing with nitrogenous fertilizers, lead to 'tetany-prone' pastures, that is, pastures on which cattle (and sheep) are likely to develop hypomagnesaemia. Head and Rook (1955) have suggested that the hypomagnesaemia of cows at grass, particularly during the early spring, may be due to inadequate absorption of magnesium, possibly associated with production of excessive ammonia within the rumen as a result of the high nitrogen content of young grass. There can be little doubt that this theory is incomplete and that other factors, including very probably the high potassium concentration found in growing plants, are also involved (see, for example, Kemp and 't Hart, 1957). The condition known as 'ryegrass staggers' seen in New Zealand in cattle grazing rapidly growing perennial ryegrass (*Lolium perenne*) is apparently a hypomagnesaemia.

Photosensitization. Although this condition is discussed in detail later in this chapter, it is relevant to say here that outbreaks of photosensitization associated with the ingestion of grasses and pasture legumes appear to occur mainly during periods of luxuriant growth (Hurst, 1942).

THE ACCUMULATION OF TOXIC MINERALS BY PASTURE PLANTS

Under certain conditions minerals present in the soil in a form not available to animals may be taken up and accumulated by plants in amounts sufficient to be toxic to livestock eating the plants The most important examples are copper, molybdenum, nitrate and selenium.

Copper Chronic copper poisoning from plant sources is essentially a problem with sheep in New South Wales and Victoria where the condition is known as 'enzootic jaundice' or 'toxaemic jaundice' It occurs as a result of the storage of abnormal amounts of copper in the liver and is characterized by a sudden rise in blood copper, followed in about 24 hours by haemoglobinaemia, haemoglobinuria and jaundice (Bull, 1952) In certain areas in New South Wales there are soils with a high copper content and herbage growing on such cupriferous soils is also high in copper In such places copper poisoning appears to be due to a high gross intake of copper In other areas the copper content of the soil is normal, but special climatic conditions, for example, heavy autumn rains, promote the early growth of non-gramineous plants (of which subterranean clover appears to be one of the most important) in which the copper content is high and the molybdenum content low There is no doubt that a high copper molybdenum ratio in the diet promotes accumulation of copper in the liver in ruminants (Dick and Bull, 1945), molybdenum apparently exerting some controlling effect on copper storage Dick (1953) has further shown that for molybdenum to exert this limiting effect the diet must be rich in inorganic sulphate When the sulphate content of the herbage is low, as it probably is in the stage of active growth, sheep would store copper even if the plant molybdenum content was relatively high The picture is further complicated by the fact that hepatic damage sustained as a result of consumption of plants such as heliotrope (*Heliotropum europaeum*) may also promote accumulation of copper within the liver

Sheep are peculiarly susceptible to chronic copper poisoning The addition of only very small quantities of copper to a 'normal' ration can raise the amount stored in the liver to a dangerous level if the supplement is fed for long enough and conditions are such as to promote storage Clegg (1956) has described poisoning in sheep estimated to have received weekly 5 gm of a mineral supplement containing 1,300 p p m. copper (i e 6 5 mg per week) for one year Symptoms of

poisoning may be precipitated by any fall in the plane of nutrition, by fasting or by physical effort (Bull, 1952) and may not manifest themselves until as long as two months after removal of sheep from the source of copper.

Molybdenum. Chronic molybdenum poisoning in cattle, known locally as 'teart', has been known in Somerset for over 100 years. Ferguson, Lewis and Watson (1940) first showed that the condition is related to the water-soluble molybdenum content of the herbage and that it can be induced experimentally by either top-dressing healthy pasture with sodium molybdate or by administration of the salt to cattle. The herbage in teart areas (on soils arising from the lower Lias formation in parts of Somerset, Warwickshire and Gloucestershire) contains 20–100 p.p.m. of molybdenum whereas normal herbage contains 1–3 p.p.m. (Ferguson, Lewis and Watson, 1943). The molybdenum content of teart pasture varies seasonally, being minimal during winter and rising from April to a maximum in September or October. Frosting causes an abrupt fall in the molybdenum level. Not all pasture plants accumulate the element to the same extent, clovers and Yorkshire fog (*Holcus lanatus*) appearing to contain the most (Ferguson *et al.*, 1940). Hay made from affected pasture is harmless after curing. A mild form of teart has been described in Ireland by Walsh, Neenan and O'Moore (1952) on pasture containing 5–20 p.p.m. of molybdenum, and in Manitoba by Cunningham, Brown and Edie (1953). In the latter case herbage contained 25·6 p.p.m. while harmless contiguous pasture contained 1·9 p.p.m.

The characteristic feature of teart is scouring; this symptom appears to be related to a relatively high intake of molybdenum. A small excess of molybdenum (2–25 p.p.m.) is said by Davis (1950) to be associated with deficient bone metabolism in herbivora, probably due to interference with phosphorus absorption and to stimulation of phosphorus excretion (Arrington and Davis, 1952). This effect of small amounts of molybdenum may not be confined to ruminants as Walsh and O'Moore (1953) believe that clinical rickets in foals may also be ascribed to an increase in molybdenum intake either from pasture (found to contain 5–25 p.p.m. of molybdenum) or from the dam's milk. Horses (and pigs) grazing on teart pastures have hitherto been thought to be immune to the harmful effects of excess molybdenum (see, for example, Hallgren, Karlsson and Wramby, 1954).

There seems to be little doubt that hypocuprosis observed in both sheep and cattle on pastures containing apparently adequate amounts

of copper is due to the presence in the herbage of a small excess of molybdenum (2–9 p p m) and excess sulphate (Wynne and McClymont, 1956) The sulphate, rather than the molybdenum, concentration, seems to be the critical factor in determining whether hepatic copper storage shall take place

Nitrate The nitrate content of plants is affected, not only by the nitrate content of the soil, but also by climatic conditions (Whitehead and Moxon, 1952) A surprising number of plants can accumulate nitrate in sufficient concentration to be toxic to stock when the environmental conditions are unfavourable to plant growth, Webb (1952) lists 55 species in Queensland alone Of the more common animal feeding-stuffs, oat, barley, wheat and rye hay, and maize and sorghum fodder are the most likely to give trouble It has been shown that application of the weed-killer 2,4-D (2,4-dichlorophenoxyacetic acid) to sugar-beet plants increases the nitrate content twentyfold (Stahler and Whitehead, 1950) and this has led to a great deal of emphasis being placed, particularly in the United States, on the possible danger attendant upon the use of this compound on pasture It is said that sub-lethal doses may have a similar effect to conditions of drought and may result in accumulation of toxic quantities of nitrate by pasture weeds Fertig (1954), however, states that no case of nitrate poisoning has been definitely traced to or shown to be caused by herbicidal treatment The nitrate content of plants may be very high, Bradley, Eppson and Beath (1940) state that oat hay, for example, may contain 5 per cent. The safe content of hay is arbitrarily placed at 1 5 per cent on a dry-matter basis

The toxicity of nitrate is due to its conversion, either in the plant before ingestion or within the alimentary tract of the animal, into nitrite. Nitrite absorbed into the blood-stream converts haemoglobin into methaemoglobin, a form which is incapable of transporting oxygen In moist oat hay exposed to the air maximum conversion of nitrate to nitrite was found to be reached about 20 hours after the hay had been moistened (Riggs, 1945), after this time the nitrite content declined until after about 10 days none could be detected. Barnett (1952) considers the organism responsible to be a facultative aerobe. Cattle seem to be most susceptible to nitrate poisoning possibly due to the favourable conditions in the rumen (Olson and Moxon, 1942) Lewis (1951) has shown that nitrite is an intermediary product in the reduction of nitrate to ammonia within the rumen of the sheep, above certain concentrations of nitrate the rate of reduction of nitrite to

for introduction into certain areas as pasture crops and have proved toxic to one or more animal species. Some examples are included here as a matter of interest.

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Tall Fescue lameness Tall fescue lameness or 'fescue foot' is a non-infective condition of cattle of importance in New Zealand, South Australia and parts of North America, characterized by dry gangrene of the hind feet and tail. It is caused by excessive consumption of tall fescue grass (*Festuca elatior* var. *arundinaceae*) and can be produced experimentally by grazing cattle on tall fescue pasture or feeding exclusively tall fescue (Jensen, Deem and Knaus, 1956). The syndrome so closely resembles that due to ergot poisoning that it was natural at first to assume that it was caused by infestation of the grass with the sclerotia of this fungus, but there can be no doubt that this is not so (Cunningham, 1949; Pulsford, 1950). Nevertheless chemical tests and spectrophotometric data indicate that some form of ergot is present in the grass (Maag and Tobiska, 1956). It is suggested that either the fungus is capable of developing in fescue grass in locations other than in place of the seeds or that the grass itself may, under certain conditions, accumulate ergot alkaloids.

Indigofera poisoning *Indigofera enneaphylla* (Birdsville indigo) is a legume widely distributed in subtropical areas of Western Australia. In horses it induces a syndrome of depression and inco-ordination known as 'Birdsville disease'; it is harmless to cattle and sheep (Gardner and Bennetts, 1954). A related species *I. endecaphylla* (Creeping Indigo), was introduced into the Hawaiian Islands as a pasture legume. Its use has been hampered by the presence in it of a toxic factor which causes loss of appetite, apathy, delayed oestrus and sometimes abortion

poisoning may be precipitated by any fall in the plane of nutrition, by fasting or by physical effort (Bull, 1952) and may not manifest themselves until as long as two months after removal of sheep from the source of copper.

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ammonia becomes limiting and nitrite accumulates. The capacity of the rumen to detoxify nitrite or nitrate appears to be reduced considerably when feeding is poor (Holtenius, 1957).

Selenium. In certain parts of the world, notably the Great Plains area of the north-western United States and western Canada, selenium occurs in the soil in forms directly available to plants. Only a few weeds, confined almost entirely to the seleniferous areas (and therefore referred to as 'indicator plants'), are able to assimilate it and to accumulate it within their tissues. In the United States the genera implicated include *Astragalus, Stanleya, Oonopsis* and *Xylorrhiza*. The decomposition products of these indicator weeds contain selenium in a form available to other species normally grown as forage crops. It is thus possible, for example, for cereal crops in such areas to produce grain containing toxic amounts of selenium.

Seleniferous vegetation occurs almost exclusively on soils derived from Cretaceous shales or limestone. Walsh, Fleming, O'Connor and Sweeney (1951), who have described selenium intoxication of stock in Eire, believe that pyritiferous shales may be a rich source of selenium. No relationship appears to exist between the amount of selenium in the soil and that taken up by any given plant species. The factors controlling the degree of absorption are not fully understood, but include such things as the chemical form of the selenium, the amount of rainfall or irrigation and the sulphur:selenium ratio (the amount of soluble sulphate present is particularly important, sulphate reducing selenium absorption).

The organic selenium compounds occurring naturally in seleniferous plants and grains are said to possess the highest toxicity of all selenium derivatives. In the United States the marginal level in herbage is stipulated as being 5 p.p.m. of the element, but even smaller amounts in the diet of a hen will depress the growth rate of chicks hatching from her eggs (Paley, Wilson, Moxon and Taylor, 1941). Indicator plants commonly contain 2,000–6,000 p.p.m.

The exact mechanism of the toxic action of selenium is not understood. It possibly replaces sulphur in the amino acids present in certain essential enzymes. The problem of selenium poisoning has been reviewed in all its aspects by Moxon and Rhian (1943).

MISCELLANEOUS CONDITIONS

A number of instances are on record of what might be termed 'pastoral *faux pas*'. Grasses and legumes have been selected as suitable

for introduction into certain areas as pasture crops and have proved toxic to one or more animal species. Some examples are included here as a matter of interest.

Phalaris staggers. In certain parts of South Australia where the perennial grass *Phalaris tuberosa* predominates in the pasture, a 'staggers' syndrome, characterized by nuclear inco-ordination and hyperexcitability, is seen in sheep and cattle grazing on the early growth following the first rains (MacDonald, 1942). The cause of the disease is unknown but it is assumed that a neurotoxic principle, which has as yet avoided isolation, is present in the plant. The condition can be prevented by weekly drenching with cobalt sulphate (7 mg. Co per head per week) but not by monthly drenching or parenteral administration (Lee and Kuchel, 1953). It was suggested that the protective effect of cobalt is due to its incorporation into vitamin B_{12} in the rumen; however, relatively massive parenteral doses of this vitamin are without effect (Australia, 1954).

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in heifers fed a diet consisting mainly of this plant. The toxic principle has been shown to be β-nitropropionic acid (Cooke, 1955) although the toxic effects produced by the plant in rabbits are considered not to be due to this compound (Hutton, Windrum and Kratzing, 1958). Its main effect appears to be to cause hepatic and renal damage (Jeganathan, 1953). *I. endecaphylla* has also been shown to reduce the growth rate of chicks (Payne and Naidu, 1955). Another species, *I. subulata*, has proved to be more promising and has been introduced into Kenya and Southern Rhodesia: it is apparently harmless to sheep (Rogerson, 1955).

Leucaenia glauca intoxication. Loss of hair in horses and pigs eating the legume *Leucaenia glauca* has been described in Hawaii, Indonesia and the Bahamas: in these areas ruminants appear to be unaffected (Owen, 1958). The toxic principle is the alkaloid mimosine. When introduced experimentally as a forage plant into the Congo, *L. glauca* proved to be toxic to sheep. As little as 500 gm. given over a period of 5–6 days brought about almost complete loss of the fleece within 15 days of the first feed, death following in some animals from haemorrhagic cystitis (Damseaux, 1956).

COMMON WEEDS OF PASTURE

Advances in research techniques during the past decade have led to the identification of the poisonous principles of some of the more common weeds.

BRACKEN AND HORSETAILS

The aetiology of bracken (*Pteridium aquilinum*) and horsetail (*Equisetum*) poisoning in the non-ruminant has been elucidated. Evans, Jones and Evans (1950) demonstrated the presence in bracken of a thiaminase, an enzyme destroying vitamin B_1 probably by cleavage of the molecule at the methylene bridge joining the pyrimidine and thiazole parts of the molecule. A similar enzyme has been shown to occur in various species of *Equisetum* and in the fern *Dryopteris filix-mas*. The syndrome of 'bracken staggers' in the horse has been established as primarily a thiamin deficiency and can be cured by parenteral administration of this vitamin. Cattle do not respond to thiamin therapy and the course of the disease in this species is quite different from that in the horse (Evans, Evans and Hughes, 1954). The essential lesion is said to be bone marrow damage affecting the megakaryocytes,

the primitive white cells and the primitive red cells, this leads to thrombocytopenia and leucopenia (Naftalin and Cushnie, 1954) The syndrome therefore resembles closely the second stage of 'radiation sickness' in man The toxic factor to the bone marrow in ruminants is considered by Thomas, Watkin, Evans and Evans (1955) to be a substance of low molecular weight and quite distinct from thiaminase It has been successfully concentrated from bracken fronds (Evans, Evans, Thomas, Watkins and Chamberlain, 1958, Evans, Evans, Chamberlain and Thomas, 1959) but has not yet been identified

Evans, Evans, Edwards and Thomas (1957) and Evans, Thomas, Evans and Edwards (1958) report successful use of butyl alcohol (α-octadecyl-glycerol-ether) in the treatment of bracken poisoning in cattle This alcohol is found in the non-saponifiable fraction of extracts of yellow bone-marrow, spleen, liver and aorta

Bracken and horsetails are dangerous when fresh and when cut green and subsequently dried. Horsetails in hay may retain their toxicity for at least 16 months (Forsyth, 1954)

BUTTERCUPS

Fresh buttercups (*Ranunculus* spp) contain an irritant, poisonous, yellow volatile oil, protoanemonin, liberated enzymically from a glycosidic precursor (ranunculin) when the tissues of the plant are crushed (Hill and Heyingen, 1951) There is still some controversy with regard to the importance of buttercup poisoning Shearer (1938), who attempted to assess the toxicity of various species, doubted if death from uncomplicated buttercup poisoning ever occurred and he is supported by Graf (1952) who found that crowfoot (*R acer*) is regularly grazed by Swiss cattle without harm Forsyth (1954), on the other hand, describes acute poisoning from *R. sceleratus* (the celery-leaves buttercup) in heifers and *Ranunculus* species also appear to be responsible for losses in the U S S R (Bolshakov, 1955) Svanberg, Åberg and Steen (1956) believe that, in Sweden, lymphoid leucosis in cattle is associated with the ingestion of *Ranunculus* and other species containing protoanemonin. The celery-leaved buttercup is that most likely to give trouble since it often provides lush greenstuff when the rest of a pasture is comparatively bare

UMBELS

The family Umbelliferae includes important and highly dangerous species. Although it is usually considered that poisoning in cattle

from hemlock (*Conium maculatum*) occurs only when other vegetation is scarce, Penny (1953) has described several cases in spring when plenty of alternative and palatable food was freely available. The roots of water hemlock (*Cicuta virosa*) and hemlock water dropwort (*Oenanthe crocata*) are exceedingly toxic and may cause fatal poisoning when unearthed during ditching and drainage operations (Milne, 1945; Crowley, 1949; Priouzeau, 1951; Janowski and Lewandowski, 1955; Wilson *et al.*, 1958). The active principle of both these plants is a long-chain acetylenic alcohol. The exotic species *Ferula communis* is of interest in that the toxic agent resembles that of spoiled sweet clover in lowering the prothrombin level and consequently increasing the blood coagulation time (Salvatore and Giovanni, 1951). *Chaerophyllum temulum* (rough chervil) is reported as having caused fatal poisoning in nutria (Krahnert and Kupky, 1953).

RAGWORT

Senecio jacobaea (Ragwort) is considered to cause more annual loss to the livestock industry than all other plants put together (Forsyth, 1954). The plant is usually avoided by grazing animals and, in consequence, reseeds itself until it almost replaces the original grass of the pasture. Most *Senecio* species appear to be harmful. The toxic factors are alkaloids of the pyrrolizidine group. Similar compounds have also been found in two genera, *Heliotropium* and *Trichodesma*, of the Boraginaceae, and in several species of *Crotalaria* (Leguminosae). All have hepatoxic properties.

Senecio species are poisonous when fresh, when dried and made into hay or otherwise processed (Cockburn *et al.*, 1955) and when ensiled (Donald and Shanks, 1958). Vardiman (1952) claims that silage can be prepared from *S. ridelli* which is non-toxic.

There is controversy as to the susceptibility of various species to ragwort poisoning: it is often maintained that sheep can be grazed upon ragwort without harm. Bull (1955) considers that the immunity of the sheep to *Senecio* alkaloids is only relative since if such animals consume ragwort for any length of time the characteristic liver lesions can be demonstrated even though there are no clinical signs of poisoning.

Ragwort poisoning is usually chronic and is associated with profound changes in the anatomy of the liver. Microscopically there is characteristically a combination of haemorrhage, necrosis and cirrhosis. Bull (1955), who has made a detailed study of the histology of the liver

of sheep poisoned with *Heliotropium europaeum*, considers that, in this species, the characteristic change is an enlargement of the parenchymal cells throughout the liver, a phenomenon which he terms 'magalocytosis' According to Bull, haemorrhages, cell necrosis and fibrosis are commonly associated changes but are not specific Hill and his colleagues (Bras, Berry and Gyorgy, 1957, Hill Stephenson and Filshie, 1958), on the other hand, believe that the pyrrolizidine alkaloids bring about an initial overgrowth of connective tissue of the hepatic veins causing partial or complete occlusion the ultimate result is a generalized fibrosis of the liver.

Other weeds either native to Britain or found as escapes which are on record during recent years as having caused poisoning are *Arum maculatum* (lords-and-ladies cuckoo-pint) (Tomaselli, Lanfranchi and Grigani, 1954, O'Moore, 1955*a*), *Arenaria serpyllifolia* (thyme-leaved sandwort) (Chapron, 1951), *Lychnis githago* (corncockle) (Placidi, 1954), *Mercurialis annua* (annual mercury) (Barron, 1944, Polidora and Maggi, 1954, Bokori, Kovács and Haraszti, 1955), *Colchicum autumnole* (autumn crocus) (Ursiny and Krchňavý, 1952), *Rumex ocetosa* (sorrel) (Coward, 1949), *Digitalis purpurea* (foxglove) (Parker, 1951), *Atropa belladonna* (deadly nightshade) (Smith, Taussig and Peterson, 1956), *Solanum dulcamara* (woody nightshade) (Greer, 1947), *S nigrum* (black nightshade) (Gunning, 1949) and other Solanaceae (Case, 1956)

TREES AND SHRUBS

YEW

The yews (*Taxus baccata* and varieties) are the most poisonous of the trees and shrubs native to the British Isles. The active principle, the alkaloid taxine, is found in all parts of the tree and is not destroyed by drying or storage. Death usually occurs very rapidly from stopping of the heart. Recovery from yew poisoning has been described (Knowles, 1949) and Edwards (1949) goes so far as to say that 'yew is not in reality as toxic for cattle as it is generally regarded' It seems likely that the explanation in such cases is that only small amounts of yew have been eaten and have become 'diluted' with the contents of the rumen.

OAK LEAVES AND ACORNS

Poisoning by green oak leaves is sometimes seen in spring when grass is scarce, but unripe acorns are a much more common source of

trouble, particularly in cattle, which seem to develop a craving for them. Acorns can be (and often have been) fed to pigs with impunity, provided they are introduced into the diet gradually and are not fed to excess. It is generally considered that it is the high tannin content which is responsible for the toxicity of both oak leaves and acorns (see, for example, Marsh and Marsh, 1919). Clarke and Cotchin (1956), although unable to demonstrate in acorns the presence of any substance other than tannin which was lethal to mice on intraperitoneal injection, believe that something apart from mere oral ingestion of tannin is concerned in acorn poisoning. Poisoning has been described during recent years in sheep (Robins and Shapcott, 1954; Mullins, 1955, and in cattle (Towers, 1950; McNiven and Grant, 1956).

LABURNUM

After the yew, laburnum (*Cytisus laburnum*) is the most poisonous tree found in Britain. The flowers and seeds are particularly toxic, but all parts of the tree contain the active alkaloid, cytisine. Whitty (1948) points out that consumption of leaves and twigs by ruminants is not invariably followed by symptoms of poisoning.

RHODODENDRON

Rhododendrons and allied cultivated shrubs (Kalmia, Azalea, etc.) belonging to the family Ericaceae contain the toxic glycoside, andromedotoxin. Although the danger to stock from these species has been known for many years it does not seem to be sufficiently widely recognized. As Bolton (1955) points out, losses in sheep from this source could be avoided if the indiscriminate planting of rhododendron bushes in hill sheep districts were to cease. Poisoning by these species is characterized by vomiting even in ruminants. Symptoms observed in sheep have been described in detail by Hignett (1951) and Pritchard (1956).

FORAGE CROPS

MUSTARD

All crucifers contain volatile isothiocyanates or mustard oils. Their distribution has been studied by Jensen, Conti and Kjaer (1953) and Kjaer, Conti and Larsen (1953). Allyl isothiocyanate, the mustard oil *par excellence*, is known to occur in black mustard (*Sinapis nigra*) and in the varieties of *Brassica oleracea* (cabbage, kale, cauliflower, etc.).

Contrary to popular belief, the seeds of rape (*B. napus*) do not contain allyl isothiocyanate but mainly 3-butenyl isothiocyanate (Kjaer, Conti and Jensen, 1953). White mustard (*Sinapis alba*) contains *p*-hydroxybenzyl isothiocyanate and a trace of isopropyl isothiocyanate (Kjaer and Rubinstein, 1954).

The isothiocyanates occur in plants in the form of glycosides from which they are released by enzymic decomposition. White mustard (like the allied weed, charlock, *Sinapis arvensis*) is harmless until the seeds have formed, when it can become dangerous (Gallie and Paterson, 1945). The mustard oils are very irritant and may cause acute gastro-enteritis if ingested. They may be at least in part responsible for the haematuria sometimes seen in stock folded on cabbage rape and kale.

KALE

Astwood, Greer and Ettlinger (1949) have isolated from the seeds of various *Brassicae* (kale, rape, cabbage, turnips, etc.) an antithyroid compound which they showed to be 1-5-vinyl-2-thiooxazolidone. The goitrogenic factor is also present in the leaves and stems (Shand, 1952; Spisni and Garavaglia, 1954). Sinclair and Andrews (1954) have described a typical outbreak of goitre accompanied by heavy neonatal mortality (and with a significant increase in the duration of pregnancy in the dams) in lambs born to kale-fed ewes.

The syndrome most commonly associated with the prolonged feeding of kale is so-called 'kale anaemia' (Rosenberger, 1943). The first symptom to be seen is a haemoglobinuria and this is accompanied by a fall in the red cell count from 6 to 1·5–2 million. Cohrs (1943) believes that the primary action of the as yet unidentified toxic factor is to cause haemolysis. What may prove to be a related condition has been described in chickens which had been allowed to run on rape pasture (Hall, 1954): here the principal lesion appeared to be a failure in blood coagulation. A macrocytic anaemia in cattle grazing rape has been reported by Evans (1952). Angelo (1951) holds the scarcely realistic view that the condition of kale anaemia is allergic in nature and due to an unknown substance in the seeds.

RAPE

Cases of poisoning in cattle folded upon rape are reported with increasingly greater frequency. The symptoms vary, some cases showing acute pulmonary emphysema and oedema, and others haemoglobinuria, nervous derangements and blindness. Coté (1944) has

described the various forms in detail. The lesions found at autopsy suggest that some inflammatory agent is responsible. Coté states that rape which shows purple discoloration is dangerous, but Evans (1951) denies that purpling or frosting can be constantly incriminated. Rape-seed meal may cause intoxication either because of its content of volatile isothiocyanate or of the antithyroid substance mentioned above.

BEET-TOPS

The dangers of allowing stock access to the fresh green tops of beet and mangolds (*Beta vulgaris* subspp.), and, of course of the *Brassicae*, turnips and swedes, are well known. It is usual to attribute poisoning to the high oxalate content of the green leaves. Baker and Eden (1954) have studied the oxalate contents of the leaves of mangolds and sugar-beet. In all varieties the total oxalate present was greatest in the summer months, the amount gradually diminishing as the season advanced. Typical values found were up to 9 and 12 per cent (on a dry-matter basis) in sugar-beet and mangold leaves respectively in July, these levels falling to 3 per cent in midwinter. Approximately one-third of this was water-soluble oxalate. Wilting, which is believed to render the leaves harmless, was found by Baker and Eden to cause a small reduction in the soluble oxalate content of the leaves. The insoluble oxalates were, in general, apparently unaffected by wilting but sometimes showed an apparent increase in amount. These authors suggest that the undesirable effects which sometimes result from feeding beet leaves may be due not to oxalate but to other unknown factors which are labile during wilting.

The high water content of beet tops is said to be sufficient to cause scouring (Gregory, 1952), but it is evident that factors other than the water content are involved in many of the outbreaks of intoxication recorded. Venn (1952), for example, describes how cattle which ate the actively growing tops of fodder-beet not only scoured but became blind. Freudenberg (1955) believes that the feeding of fresh or ensiled sugar-beet leaves in certain parts of central Germany is associated with the increased incidence of puerperal haemoglobinuria seen in cattle in these areas. Freudenberg states that saponins are present in the leaves and that these, together with hypophosphorosis due to the unsatisfactory calcium:phosphorus ratio of the diet, are responsible for the condition. It is interesting in this connection to note that Parkinson and Sutherland (1954) suggest that puerperal haemoglobinuria may be due to a

phosphate deficiency as a predisposing factor and the feeding of kale as the precipitating cause

Sugar-beet tops are peculiarly toxic to horses, hundreds having been said to have died in Europe from the effects of eating the ensiled tops The toxin causes progressive bulbar paralysis, Hutyra, Marek and Manninger (1938) state that a similar syndrome is seen in turnip poisoning in horses

CEREALS

Grazing of winter-sown wheat and other cereals not infrequently leads to a condition in cattle sometimes known as 'wheat-pasture poisoning with symptoms characteristic of a hypocalcaemia A study of the chemistry of the blood serum in such cases has shown that there is indeed a decrease in both the total and diffusible calcium accompanied by a fall in inorganic phosphate and magnesium and an increase in the total protein, globulin and possibly potassium levels (Crookshank and Sims 1955) The aetiology of the condition is obscure.

Young green cereals (oats and barley) are strongly rachitogenic (Ewer and Bartrum 1948) There is adequate calcium and phosphorus in the offending plants and supplementary feeding of calcium and/or phosphorus does not prevent the disease Ewer (1950) therefore postulated the existence of a conditioning factor' in the young oat plant which specifically interferes with the uptake of phosphorus The presence of a rachitogenic factor has been demonstrated by Grant (1951) and it has since been isolated and identified as carotene (Grant 1953) Grant suggests that the ricket inducing effect of winter green feed on sheep is due to the high carotene intake at a time of the year when the vitamin D status of the animal is normally low

SWEET CLOVER

The story of 'sweet clover disease' is now well known and it is necessary only to mention briefly the circumstances which attend development of the condition The toxic principle is dicoumarol a substance which is formed in sweet clover (*Melilotus* spp) under certain conditions as when the plant is damaged by weather is badly harvested or when hay becomes mouldy Dicoumarol is believed to interfere with prothrombin production in the liver and the primary lesion of sweet clover disease is haemorrhagic diathesis leading to haemorrhages all over the body Cattle appear to be most susceptible to dicoumarol

poisoning probably because they will accept hay or silage when it is so spoiled that other animals refuse it.

For a detailed account of the events leading to the isolation of dicoumarol and to the study of its physiological action the reader is referred to the series of papers published by K. P. Link and his associates in the *Journal of Biological Chemistry* from 1940 onwards.

ROOTS

MANGOLDS, ETC.

Freshly lifted mangolds are dangerous because of their high content of nitrate (see, for example, O'Moore, 1955*b*). This may be as much as 7 gm. per kg. (Robinson, 1942). Under certain conditions of storage and preparation, this nitrate is spontaneously converted to nitrite, a highly toxic substance. Robinson (*loc. cit.*) has described how 200 of a herd of 600 pigs died within a short time of being fed cooked, freshly pulled mangolds. A considerable amount of nitrite (0·13–1·15 per litre of nitrite N) was found in the cooked mangold mixture. MacIntosh, Nielson and Robinson (1943) state that nitrite formation can be avoided by cooking for at least 2 hours at or near the boiling point. Turnips and swedes may cause trouble for the same reason.

Mangold roots, as well as the leaves, may contain oxalate and when castrated sheep or cattle are fattened on rations containing mangolds, especially when the latter have been grown on calcareous soils, obstruction of the urethra by oxalate crystals has been observed.

Many of the digestive disturbances and some of the fatalities seen in ruminants fed roots can be attributed to over-consumption rather than to oxalate or nitrite poisoning. Halnan and Garner (1940) consider that the high proportion of amides found in all strains of mangolds before frosting may be responsible. Dain, Neal and Dougherty (1955) have demonstrated the presence of histamine and tyramine in the rumen contents of sheep experimentally overfed with new wheat or cracked corn. The level of histamine in the ingesta was found to be directly related to the degree of illness exhibited by the sheep, and Dain *et al.* therefore conclude that indigestion from overfeeding in general may be attributed to the production of toxic amines. Charton (1954) and Scarisbrick (1954) suggest that the large amount of sucrose in the roots of mangolds, fodder-beet and sugar-beet, together with the high water and low protein content, induces disturbances in the ruminal

flora. Scarisbrick was able to show that overeating of mangolds (and other forage crops) may lead to production of lactic acid in excessive amounts within the rumen, the resulting fall in pH is associated with ruminal atony and symptoms of indigestion Lactic acid fermentation has also been observed in the rumen of sheep and throughout the bowel of horses allowed to gorge upon wheat (Australia, 1954) In horses this was accompanied by mild acidosis and severe haemo-concentration, some susceptible animals developed laminitis Changes in the rumen flora leading to alkalosis are invoked by Worden, Bunyan and Pickup (1954) to explain a form of hypocalcaemia seen in cows following excessive consumption of fodder-beet The overall clinical picture was similar to that of wheat-pasture poisoning discussed above There is a possible connection between the aetiology of this condition as suggested by Worden *et al* and that of hypomagnesaemia as propounded by Head and Rook (1955) A hypocalcaemia accompanied by a fall in serum potassium and a rise in inorganic phosphate levels observed in horses fed exclusively on oats has been suggested to have a different aetiology and to be mainly due to withdrawal of potassium from the body as a result of the relatively large amount of phosphorus in the diet (Neumann-Kleinpaul, Zeller and Jacob, 1954)

POTATOES

It is well known that green or sprouting potatoes should not be fed to stock because of the large quantities of the alkaloid solanine that are produced during the greening process The haulms are equally poisonous and have apparently caused considerable losses in Europe Steaming or cooking green or sprouted tubers renders them safe for animal feeding (Ironside, 1943, Temperton, 1943)

ONIONS

It is not usual for animals in this country to be fed large quantities of onions as part of their staple diet, but in certain parts of the United States it is apparently common to dispose of unwanted market crops in this way (Koger, 1956) This practice is sometimes attended by fatal consequences Poisoning from onions (*Allium cepa*) has been reported by Goldsmith (1909) in horses, by Thorp and Harshfield (1939) and Koger (1956) in cattle, and by Nordio (1952*a*) in poultry and yet the potential danger from this vegetable is by no means generally recognized. Haemoglobinuria, anaemia and jaundice are constant signs of poisoning in mammals Kobayashi (1950) has also described

degeneration and necrosis in the parenchymatous organs with mycloid metaplasia in cases of chive (*Allium schoenoprasum*) poisoning in horses. Nordio (1952*a*, *b*, *c*; 1953*a*, *b*) has studied the haematology of onion poisoning in various species. He made the interesting observation (Nordio, 1952*c*) that the anaemia develops more slowly in the dark. There is some doubt if it responds to vitamin B_{12} therapy (Nordio, 1953*b*, *c*). According to Koger (1956) chemical tests indicate that the toxic principle is an alkaloid.

PHOTOSENSITIVITY

The condition of photosensitivity is induced in an animal by the presence in its peripheral blood of a substance (a so-called 'photodynamic agent') which is capable of absorbing light strongly and passing on the energy in such a way as to cause a pathological reaction within the tissues. When a photosensitized animal is exposed to light of the specific wavelength absorbed by the photodynamic agent a syndrome characterized by a dermatitis and/or a conjunctivitis (and in some cases hyperaesthesia) develops; this syndrome is known as photosensitization (Clare, 1952).

The photodynamic agent in cases of photosensitivity from plant sources may be either a substance present in the plant which is absorbed from the gut and passes into the peripheral circulation (giving rise to 'direct photosensitivity') or a substance which is normally formed during the course of digestion but which finds it way into the peripheral blood-stream only if the liver is damaged (causing 'hepatogenous photosensitivity'). In the latter case the photodynamic agent is almost invariably phylloerythrin, a breakdown product of chlorophyll (Rimington and Quin, 1934; Quin, Rimington and Roets, 1935).

It seems likely that a pure 'direct' photosensitivity is seen in only a few isolated cases; the syndrome of photosensitization is almost always associated with some degree of liver damage probably caused by a 'hepatoxin' in the plant. The plant species which have been shown unequivocally to contain a photodynamic agent are *Fagopyrum esculentum* (Buckwheat) (Chick and Ellinger, 1941) and *Hypericum* spp. (St. John's Wort) (Pace, 1942). Buckwheat meal has been shown to give rise to liver cirrhosis (Kubo, Fujimoto and Nakayama, 1938; 1939) so that photosensitivity from *F. esculentum* may be partly hepatogenous.

The classical instance of hepatogenous photosensitivity is, of course, offered by *Tribulus terrestris*. The wilted vegetation of this South

African fodder plant was shown by Theiler (1918) to be responsible for the condition known as *geeldikkop* in sheep The nature of the hepatoxin is not known Other plants known or believed to induce hepatogenous photosensitivity are numerous The most important form of this type of photosensitivity is undoubtedly 'facial eczema', a condition which sporadically affects sheep in New Zealand, the plant concerned is perennial ryegrass (*Lolium perenne*) (Cunningham, Hopkirk and Filmer, 1942) The liver lesion is essentially cholangitis of the smaller ducts The ability of the grass to give rise to hepatic lesions when fed has been associated with the presence of spores of *Sporidesmium bakeri* (Percival and Thornton, 1958) and a hepatoxin has been isolated from the fungus which is capable of producing facial eczema disease in sheep (Thornton and Percival, 1959) Climatic factors are believed to be largely responsible for development of potential toxicity (Levy and Smallfield, 1942) Filmer (1955) has pointed out that, by adopting simple precautionary measures, outbreaks of facial eczema can be prevented

Many fodder legumes including lucerne, clovers and vetches, may also give rise to photosensitivity in horses and cattle leading, on exposure to light, to the syndrome known variously as 'trifoliosis', 'trefoil dermatitis' or 'clover disease' Clare (1952) considers that this may be a form of primary photosensitivity, but there is ample evidence to show that horses grazing upon these plants may develop hepatic cirrhosis, or 'big-liver disease' (Schimke, 1950, Forsyth, 1954), which suggests that the photosensitivity may be hepatogenous in origin. There is little definite evidence regarding the conditions leading to development of potential toxicity in these otherwise useful pasture plants

A number of other conditions which seem to be associated with a photosensitivity have been described in stock in the British Isles Lamont (1952) has referred in detail to two in particular affecting cattle and horses respectively and known in Northern Ireland as 'brown nose' or 'copper nose' and 'blue nose' Their aetiology is unknown, but they occur during the grass season The only British plant species which can be implicated definitely in production of photosensitivity is *Narthecium ossifragum* (Bog asphodel) sheep are affected and the syndrome is associated with hepatogenous jaundice (Endo, 1955) Photosensitivity is not confined to mammals Collet and Henry (1952–3) have described a typical photosensitization syndrome to ingestion of buckwheat in turkeys

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CHAPTER TWENTY-NINE

Herbicides

E. F. EDSON

General considerations—The 'Hormone-type' selective herbicides (2,4-D, MCPA, MCPB, 2,4-DB, 2,4,5-T, CMPP and TBA)—Borates—Dichloropropionic acid (Dalapon)—Aminotriazole—Dinitro-butylphenol—Accidental contamination of pastures or hedges by potato-haulm destroyers and by insecticides.

Although there is vast usage of selective herbicides for the control of broad-leaved weeds in cereals in this country, there is as yet comparatively little routine use of such material in pasture improvement. Chemicals are readily available which will eradicate most of the weeds of pastures, but reluctance to use them comes from several causes. First, farmers and advisory services are not yet convinced that control of weeds in a reasonably good pasture is economically worth while: indeed, some believe that the existence of a reasonable weed population is good for the animals' nutrition, milk production and milk quality, a view widely held on the Continent. Second, many of the 'hormone-type' selective weedkillers, widely used in cereal crops, are apt to cause some degree of damage to clovers in the pasture. Those least harmful to clovers, e.g. MCPB and 2,4-DB, are somewhat unreliable in their control of the major weeds. Another effective herbicide for cereals undersown with clover, or new or reseeded pasture, is dinitro-butylphenol (DNBP, dinoseb). This chemical is very active against most annual broad-leaved weeds, but nearly harmless to clovers. Unfortunately, DNBP, like the closely related chemical dinitrocresol (DNC) is a vivid yellow dyestuff of rather high toxicity to man. Somewhat tedious safety measures are therefore required in its use. The most generally satisfactory selective herbicide for use on pastures, with only

slight effects on clovers, is the hormone-type material MCPA, which when specially formulated to give increased selectivity, can make a considerable improvement to weedy pastures. Although removal of the weeds undoubtedly improves quantity and quality of the remaining grasses and clovers, with increase in starch equivalents, it is not generally accepted that these improvements are always worth the effort and cost involved.

The control of such tough, dominating weeds as bracken, rushes, hawthorn scrub or docks is usually worth while. The improvement of such marginal or newly reclaimed pasture is often helped by the use of aggressive forms of the hormone weedkillers, e.g. 2,4,5-T or 2,4-D. A number of other chemicals have had experimental usage for special purposes, e.g. aminotriazole, dalapon and borates.

Agricultural spray chemicals may occasionally reach pastures by the drift of spray mist from adjacent operations on other crops. The use on neighbouring fields of such toxic chemicals as arsenites, and some organophosphorus and chlorinated hydrocarbon insecticides, may therefore contaminate pastures or intervening hedges to a dangerous degree. Although the actual concentration of such toxic chemicals on the grazed vegetation may be quite small, the fact that a dairy cow may eat up to 200 lb., or about one-quarter of its body-weight, of fresh vegetation in one day means that comparatively large amounts of chemical may be ingested in this way.

Fortunately, there is a considerable amount of information on the toxicity and toxicology of the pesticides likely to be used for pasture improvement, or likely to contaminate pastures or hedges, so that adequate advice on safety precautions can be offered. Similarly, the normal development of a new pesticide involves the development of a sensitive analytical method, so that the pesticide manufacturer is usually both willing and able to help in any such problem.

THE 'HORMONE-TYPE' SELECTIVE HERBICIDES

These are synthetic organic chemicals, mainly substituted phenoxyacetic propionic or butyric acids, used as either alkaline salts, or as esters. They are applied at comparatively low dosage rates, of 1–2 lb. active chemical per acre, dissolved in water. The common designations for the most important members of this group are 2,4-D, MCPA, MCPB, 2,4-DB, 2,4,5-T, CMPP and TBA.

All these chemicals are of very low toxicity to mammals and other

vertebrate organisms. Their great toxicity towards plant life is therefore extremely selective. They have been known, experimented on, and used for periods up to fifteen years, and even in Britain up to three million acres of cereal crops are treated with such materials in every year. There has thus been ample chance for unforeseen adverse effects to arise, if such were latent. In practice, the hormone weedkillers have caused virtually no adverse effects on farm stock, wild life or humans, despite the fact that no specific safety precautions in handling or use have been taken (except to avoid drift on to susceptible broad-leaved plants). The same general freedom from adverse effects has occurred in North America, where the hormone weedkillers (mostly 2,4-D) have had intensive use for more than a decade.

The following studies have done much to confirm that the hormone-type weedkillers offer virtually no risk to farm stock.

Rowe and Hymas (1954) made a detailed laboratory and field study of the toxicity of 2,4-D, and 2,4,5-T and MCPA to small animals and cattle. They concluded that the acute oral LD 50 values of these materials in animals were in the range 300–1,000 mg./kg., i.e. they were virtually nontoxic in practice. This applied to both pure materials and to commercial formulations. Their chronic dietary toxicity and ingestion hazards to farm stock, based on the results from

of important herbicides including 2,4-D, 2,4,5-T and DNBP, to 3-acre plots of alfalfa and brome grass Half each plot was sprayed on the first day, the other half 7 days later. Horses, cattle, sheep, pigs and poultry were ascribed to each plot, and remained on it through both sprayings and for many weeks afterwards The chemicals were applied at 2–4 times the normally recommended dosage rates

Observations were kept on stock health, weight change and grazing preferences, and on fodder analyses The authors concluded, quite simply, that 'the results of this experiment indicate that none of the herbicides used had any serious physiological effects on the livestock involved' This work is particularly useful in that it strongly suggests that livestock need not be removed from fields during treatment with these pasture herbicides

Carey (1956) studied the more recent herbicide 2,4-DB, and found its acute oral LD 50 to be approximately 700 mg /kg (rat), 300 mg /kg (rabbit), 500 mg /kg (guinea-pig) and over 450 mg /kg (hen) No toxic effects were seen after administration of half the above dosages Female rats receiving 1,000 p p m in the diet for 63 days showed weakness and reduced weight gain, trace effects occurred at 200 p p m , but no effects were detectable at 40 p p m for 63 days Work in the same laboratory showed that another recent herbicide, MCPB, was also of very low mammalian toxicity, with acute oral LD 50 values of 600–1,500 mg /kg , and little evidence of any cumulative toxicity from repeated non-fatal injections daily, or when incorporated at tolerable levels in the diet

Edson (1958) investigated the toxicity of trichlorbenzoic acid (TBA), used since 1957 to control some important hormone-resistant weeds of cereals, and found it also to be virtually nontoxic Acute oral LD 50 values ranged from 300 to 1,500 mg /kg , depending on species Dietary toxicity tests on rats for two months showed that 100 p p m was entirely harmless, 1,000 p p m. caused slight toxic effects on kidney and liver, but even 10,000 p p m , although causing some weakness, weight loss and kidney injury, was non-lethal after two months' feeding

One unusual aspect of the hormone weedkillers' properties must now be referred to For many years, it has been widely believed, and stated, that the initial effects of these chemicals on poisonous weeds of pastures result in their greater palatability to stock, and greater chance of causing farm stock casualties Most manufacturers advise that stock should not be allowed to graze fields severely infested by poisonous

weeds for two weeks after spraying. There has been some attempt to explain these effects by an increase in sugar content, or nitrate build-up after spraying, but the scientific evidence is somewhat vague. Ragwort is a particularly important weed in this respect, but no doubt others are also important. An incident in 1958 reveals that there is a real possibility of unforeseen effects of this type. A herd of dairy cattle was allowed into a salt marsh in Devon, known to have many patches of hard and soft rushes, but which had been safely grazed in the same way for many years past. A few days before the herd was allowed in to the pasture, an aggressively herbicidal mixture of sodium chlorate, monuron and 2,4-D, all virtually nontoxic to stock, had been sprayed on the vegetation alongside an oil pipe-line crossing the field, and separated from it by a sound barbed wire fence. Within a few days, three of the herd had died, with stomachs full of rushes, and effects identical with those reported from rush-poisoning. Many others of the herd were temporarily ill. Examination showed that the spray had spread to a distance of about one foot inside the pasture along the fence. The only rushes showing any signs of grazing were those which had been sprayed in that strip. The circumstantial evidence strongly suggested that these rushes had partially wilted, or otherwise become more palatable than normal to the stock, some of which had then avidly grazed them, and died from rush-poisoning in con-

cause any risks to stock, as their toxicity is low. Pfeiffer, Hallman and Gersh (1945) found borates to have acute oral LD 50 levels of 1–3 gm./kg. in small animals, and that 1,000 p.p.m. in the diet was apparently harmless to experimental animals. *Dalapon* (dichloropropionic acid) is sometimes used for selective control of couch grass; it also is virtually non-toxic. Unpublished results from an industrial laboratory (Dow Chemical Company, 1955) quote acute oral LD 50 values of from 3.36 to 8 gm./kg., depending on species. In rats, 100 p.p.m. in the diet for 100 days was apparently harmless, while 346 and 1,080 p.p.m. caused slight toxic effects; 3,460 and 10,800 p.p.m. caused definite injurious effects to the liver and kidney, although non-lethal in 100 days. *Aminotriazole* has also been used experimentally in pasture improvement. Weir, Paynter and Elsea (1958) quote acute oral LD 50 values of 25 gm./kg. in rats and 14.7 gm./kg. in mice. Dietary toxicity was rather high, mainly because aminotriazole appeared to induce goitrous changes in the thyroid glands of animals receiving dietary concentrations higher than the 'ineffective' concentration of 50 p.p.m.

The presence of clovers in pastures may make it necessary to use *dinitro-butylphenol* as a selective herbicide. The dinitro- weedkillers are appreciably more acutely toxic to animals and man than most other herbicides, with oral LD 50 values of 25–50 mg./kg., depending on species. In small doses, however, toxic effects are unlikely, as these chemicals are only slightly cumulative in toxic effects. Thus Spencer *et al.* (1948) found rats able to survive 100 p.p.m. in the diet for 200 days, without detectable adverse effects. Only a proportion of the rats receiving even 500 p.p.m. for 21 days died during the trial. This restricted cumulative toxicity explains how the stock used in Grigsby and Farwell's field tests with DNBP could safely graze in DNBP-sprayed pastures. Both DNC and DNBP have been used extensively in British cereal spraying for over ten years, and there must have been many occasions when spray has drifted from the treated field on to hedges and pastures available to farm stock. It is interesting therefore that there are almost no recorded instances of fatalities from such causes, the few DNC stock casualties reported having been due to access to spillages of concentrated materials on the pasture used for filling up spraying machines, or contamination of drinking trough water, etc. Although factual data suggest that fields treated with DNBP offer little risk to grazing stock (unless deliberately excessive dosage rates are applied), it is generally recommended by manufac-

turers that stock should not be allowed entry to dinitro-treated or contaminated fields for two weeks after application.

The accidental contamination of pastures or hedges by other types of chemicals used on adjacent fields has occasionally caused stock poisoning. The most toxic materials likely to be used include sodium-potassium arsenites (potato-haulm destroyers), schradan, demeton, tetraethylpyrophosphate, parathion (organophosphorus insecticides) and dieldrin (chlorinated hydrocarbon insecticide). With the increasing use of helicopters or fixed-wing aircraft for applying insecticides and fungicides to growing crops, a rather new problem has arisen. While ground spraying machines can fill up in very limited space, usually on the field to be sprayed, aircraft must operate from some suitably flat field, usually a pasture, within easy distance. Carelessness and haste in filling up the aircraft may cause considerable spillages of chemical concentrate on the pasture. All too often, these are likely to be left unburied. Stock are thus exposed to a completely unnecessary risk of ingesting large amounts of concentrated material, and will often do so without apparent cause or provocation. In 1958, several cattle died from this cause, the chemicals concerned being copper compounds of only moderate toxicity, used as fungicides to combat severe potato blight.

In general, any farmer encountering unusual signs of poisoning in stock out to pasture, during the period May–September, should bear in mind the possibility that the animals may have bad access to toxic chemicals contaminating their grazing area from spraying operations in upwind fields, and should make enquiries on that possibility.

In summary, there is abundant evidence that the herbicidal materials recommended for weed control in pastures are most unlikely to cause risks to stock when used properly, and as recommended by the suppliers. Risks are possible from misuse, such as failure to bury spillages, or from the presence of poisonous weeds made palatable or edible by the chemical sprayed, and some precautions are needed against both these risks. Otherwise, chemicals recommended for pasture treatment are virtually non-hazardous. More toxic materials may contaminate pasture or hedges from adjacent spraying operations, and these should be regarded with some suspicion until it is assured that the chemicals used were of non-hazardous nature.

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